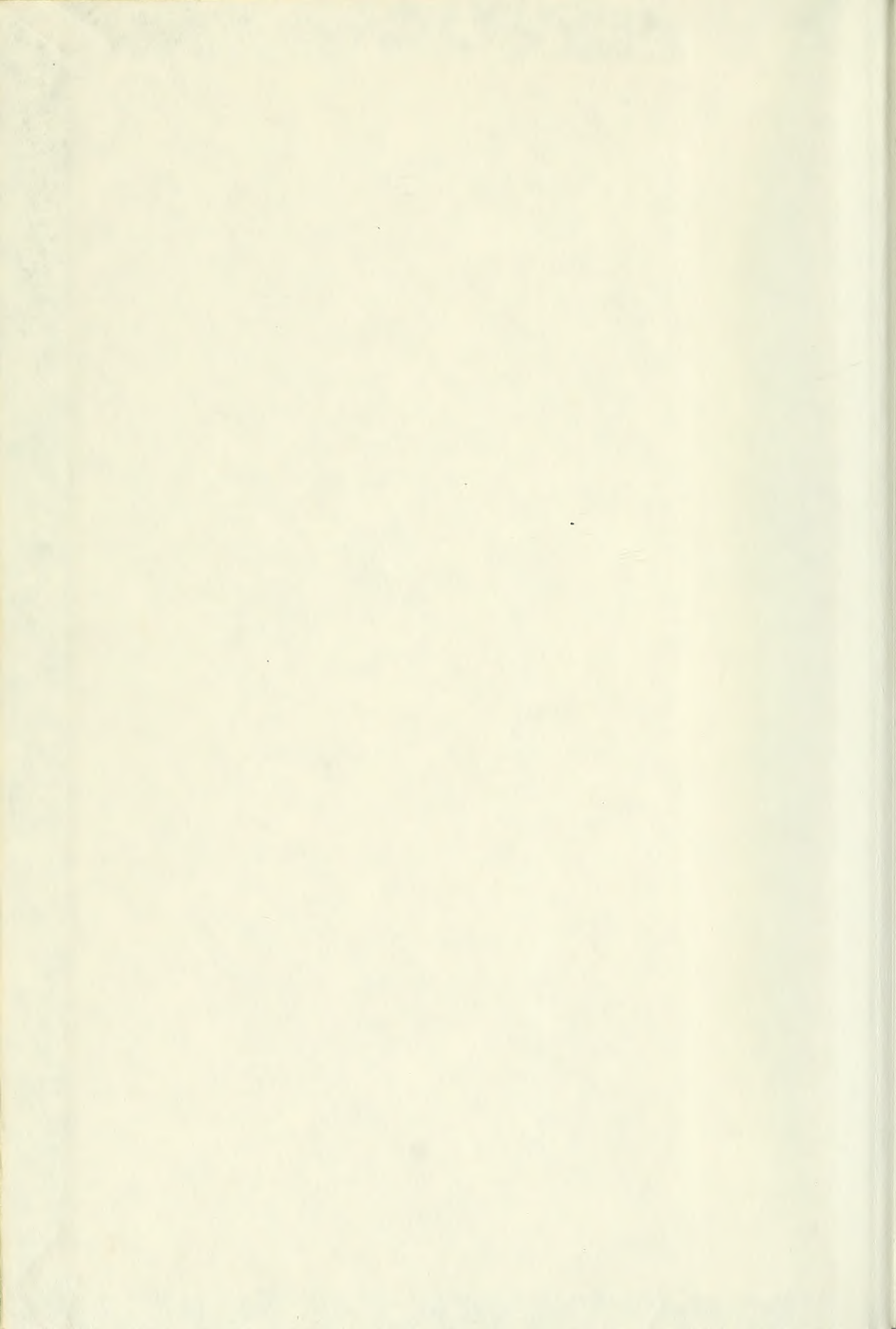
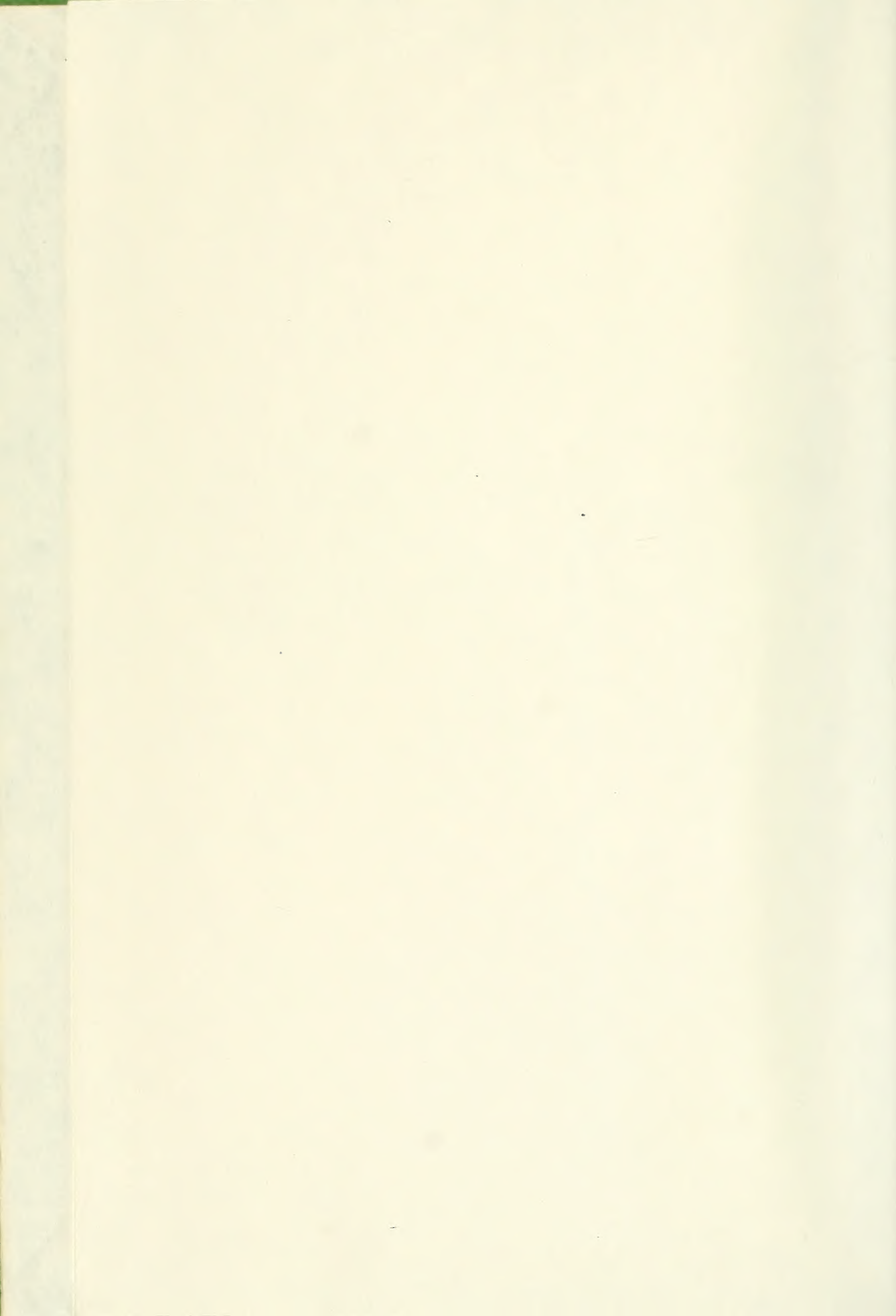


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CHANGES IN THE INTERTIDAL ALGAL FLORA OF THE
LOS ANGELES AREA SINCE THE SURVEY
BY E. YALE DAWSON IN 1956-1959

— THOMAS B. WIDDOWSON¹

ABSTRACT: Each of the 15 stations set up by Dawson between Pt. Dume and Dana Point were reoccupied two or three times during the period 1968 to 1970. The data obtained were analysed in a manner comparable to Dawson's. The most conspicuous reductions were found in the flora of stations exposed to direct human interference, and in the species which characteristically grow half buried in sand. Methods are suggested by which problems associated with sand movement, seasonal variation, and taxonomy may be minimized.

From the years 1956 and 1959, the late E. Yale Dawson surveyed the intertidal algae in southern California for the State Water Pollution [Quality] Control Board. He examined the collections which W. A. Setchell and N. L. Gardner preserved from numerous visits to the White Point area between 1895 and 1912, and from these deduced that the flora at that time contained at least 60 species of conspicuous benthonic algae (Dawson, 1965a: 223). With a view to providing an accumulation of information for future workers, Dawson set up 44 stations along the exposed rocky shores between Point Conception and San Diego (Fig. 1). These stations consisted of a fixed shore base point and a transect running down the beach at a certain bearing from this point. Dawson's published field notes (1965b), color transparencies and annotated aerial photographs (deposited in the Allan Hancock Foundation Herbarium) served to identify the base point and the bearing of each transect. His field notes provided qualitative information about the frequency of algae found during each visit in an undefined narrow strip along each transect. He visited each station between one and four times for a total of 103 visits. During each visit he made collections which he filed in duplicate under station and species in the Herbarium of the Allan Hancock Foundation. In general, these collections probably provide a more complete and accurate list of the species at each station than do the notes, but the notes provide the only information about frequency.

Dawson published two brief discussions of his results (1959a, 1965a). In these, he calculated the number of conspicuous species observed at each station, averaged over several visits (1965a, Fig. 8.1). He then assigned a numerical weight of 1 for a species reported to be rare or scant at a station for a particular visit, 3 for occasional to frequent, and 10 for common to abundant. These weights, totalled

over all visits and stations, provided the basis for a list of the "46 most common marine plants of southern California in order of their relative frequency" (1965a, Table 8.1). He also presented these weights in two large tables (1959a, Tables I and II) with 189 species on the Y-axis and a selection of station visits, grouped in four seasons, along the X-axis. He planned a more explicit analysis of seasonal variation (1959: 181) but apparently never completed this (1965a: 224).

Dawson based some of his conclusions on a comparison of his 1956-9 data with the data he derived from Setchell and Gardner's 1895-1912 collections at White Point. In the same way, the conclusions in this study are based on a comparison of Dawson's 1956-9 data with those gathered in 1968-70. These comparisons are necessarily limited by the extent and precision of the earlier study (which cannot now be improved) and by the availability of valid statistical techniques for use in making the comparison.

One long term comparison similar to the present study is that of Bellamy, Bellamy, John, and Whittick (1967). The effects of pollution along about 50 miles of the Durham and Northumberland coast are measured by a reduction of 9-70% in species number since 1861. It is only recently that other quantitative measurements, such as percentage cover and numbers of individuals per unit area, have become common practice in the study of intertidal plants. This means that comparisons using such quantitative measures are short term studies, with the earlier data taken in the recent past (Bellamy, Clarke, Jones, Whittick and Darke, 1967; Cowell, 1969). These short term studies also

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have a practical advantage over long term studies in that both the earlier and the later surveys can be made by the same observer.

Conclusions derived from the observations of populations before and after, with and without pollution, should be confirmed by experimental study of the effects of individual pollutants on individual species. The enormous number of problems here can only be reduced to manageable size by prior observational work, so it is not surprising to find that little has been done thus far. Boney (1968) investigated the effects of various detergents on *Ascophyllum*, *Cladophora*, *Bryopsis*, *Prasinocladus*, *Porphyra*, *Acrochaetium*, and *Polysiphonia*. Okamura, *et al.* (1926) correlated heavy mortality of intertidal *Porphyra* in Tokyo Bay with episodes of heavy fog. They demonstrated experimentally the lethal effect of soot particles from the fog containing 70% to <0.7% adsorbed sulfur dioxide and also of air containing more than 0.01% free SO₂.

Any survey designed to be the first part of a long term comparison study should certainly use the best current techniques, and these now include quantitative measurements and experimental work. However, it is perhaps inevitable with the development of new techniques that the person who comes to make the second part of the study should be dissatisfied with the first. In this context, it is perhaps ironic that the paper by Okamura, *et al.* (1926) should seem so contemporary.

METHODS

Choice of stations. — The 15 Dawson stations between Point Dume and Dana Point were each visited two or three times during the years 1968 to 1970. This particular set of stations is the maximum available for a study centered on Los Angeles, since a larger set would be affected by the infrequency of stations southeast of Dana Point, producing a bias in favor of the stations northwest of Los Angeles (Fig. 1). These 15 stations occur in three groups; along the Malibu coast, on the Palos Verdes Peninsula, and along the Orange County coast. They are separated by stretches of sandy beach along Santa Monica Bay and Long Beach which form a physically unsuitable substratum for large benthonic algae. The stations near Point Dume and Dana Point appear to enjoy natural conditions, while varying degrees of water and air pollution, and intensity of collecting activity, can be observed at the stations in between.

Of the 32 station visits made in this study, 16 were made by students, whose contributions are acknowledged below. Specimens were collected to substantiate each record and, in the case of student

work, were used by the author to check the identifications made. These specimens were deposited in the herbarium of the California State College at Long Beach.

Taxonomic problems. — Many intertidal algae cannot be identified to species or, sometimes, even to genus in the field. Sometimes this problem arises because such identification requires laboratory techniques, and sometimes because described species appear to intergrade or show the need for further taxonomic work in some other way. Since many of the areas studied are now marine preserves, and since indiscriminate collecting in the past may have been a factor in the decline of the algal flora, it is desirable to reduce the need for collections as much as possible in the future. Species which cannot readily be distinguished in the field have been grouped together in this study. The taxonomic categories used in analyzing both the 1956-9 and the 1968-70 data include single species (e.g. *Gigartina leptorhynchos*), pairs of species (e.g. *Gelidium coulteri* or *G. crinale*), genera (e.g. *Ulva* spp.), pairs of genera (e.g. *Gracilaria* or *Gracilariopsis*), or even larger groupings such as diatoms or blue-green algae. These groupings are listed in Table I, and are referred to as 'entities' below, wherever the word species would be inappropriate. The taxonomic system used is basically the same as that published by Dawson (1959a, Tables I and II). The marine grass *Phyllospadix* is, in effect, included with the algae in this study.

Number of species per station. — The easiest analysis of the algal flora, and the one least subject to taxonomic problems, is an estimate of the number of entities per station. Dawson (1965a, Fig. 8.1) used the arithmetic mean of his observations for stations which he visited more than once. This does not seem to be the best statistic available, since observations of this type are subject to a biased error. (It should be easier to miss a species which is there, than it is to record one which is not there.) The statistic presented in Figure 2 is the total number of entities observed during all the visits made to a station. If entity A, B, and C were observed on one visit, while entity B, C, and D were observed on a second, the number shown in Figure 2 would be 4. This is substantially the same method which Dawson himself used in analysing Setchell and Gardner's records from White Point (Dawson, 1965a: 223). This statistic will tend to increase with each successive visit, so in Figure 2 the value for 1956-9 and for 1968-70 is calculated for the same number of visits at each station. However, the number of visits used varies from station to station, so one station should not be compared with another. Dawson derived the figure of 60 species for Setchell

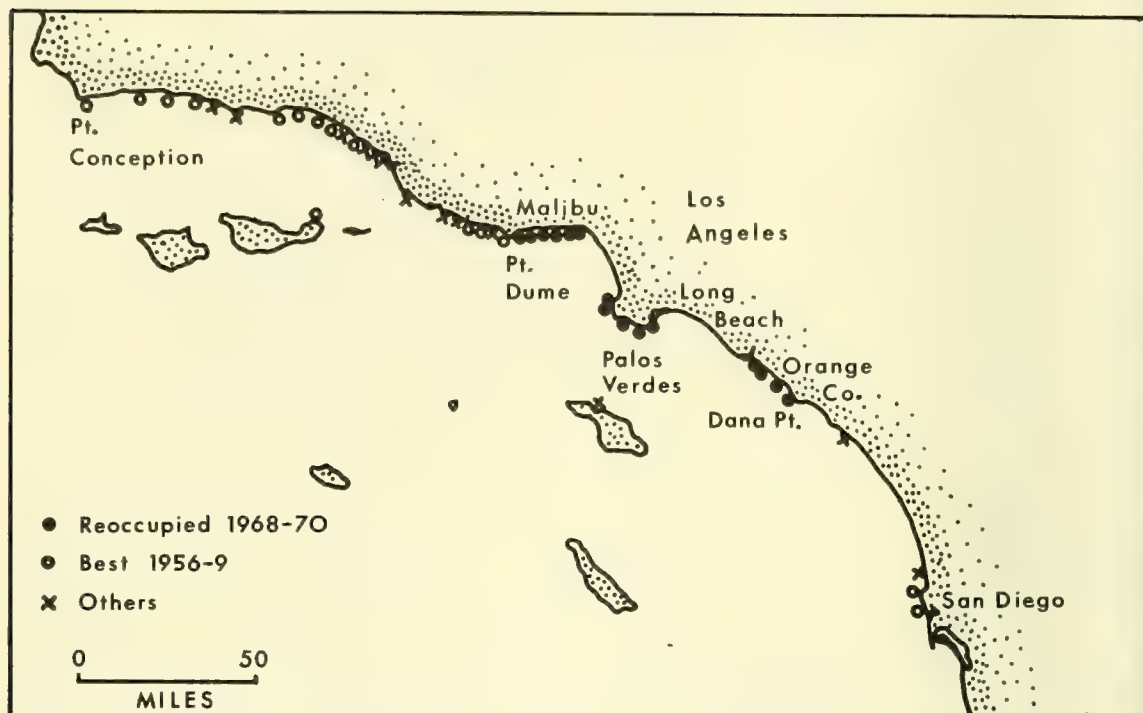


Figure 1. Stations for sampling intertidal algae, established by E. Yale Dawson during the period 1956-9.

and Gardner's collections from many visits, so it probably represents a flora not greatly larger than that found at Station 19 or 22 today.

Scoring species for frequency. — Dawson's numerical scoring for qualitative observations of frequency were changed in two ways. First, the score for 'common to abundant' was changed from 10 to 9, so that it could be accommodated in one column on the punched cards used for this analysis. Second, for each visit and species a score was assigned to each zone (upper, middle, and low intertidal, and tide pools) instead of to each station as a whole. In this way, the maximum score per entity per visit was increased from 10 to 36, and more information was derived from the original notes.

Dawson (1959a, Table I and II) tried to present variations in frequency by species, station, and season simultaneously. These modes of variation are presented separately in this study (Figs. 3 and 4, 5 and 6).

In Figure 3, the scores totalled over all stations are compared for the 10 most frequent entities, using data from the 15 stations in the Los Angeles area in 1968-70, (right), the same stations in 1956-9 (middle), and the 15 stations outside the Los Angeles area where Dawson found an average of more than 30 species in 1956-9 (left). The scales are adjusted to allow for the fact that 32 visits are involved in

the data on the right, 34 visits for those in the middle, and 39 visits for those on the left. The numbers in circles show the rank of a certain species when it is not in the top 10 for that particular column. The data on the left are included as the best available indication of the original composition of the algal flora of southern California. Total scores in the Los Angeles area for species below the top 10 are presented in Table I. The position of the stations used are shown in Figures 1, 7 and 8.

Placing species in non-taxonomic groups. — Dawson remarked (1965a), that articulated corallines increased and leafy red algae decreased in areas exposed to sewage pollution. In Figure 4, the total scores for a number of such groupings are shown. Data from Dawson's best 15 stations outside the Los Angeles area (A), Dawson's 15 stations in the Los Angeles area (B), and these same stations during the period 1968-70 (C) are compared in the same way as in Figure 3. The values for the Los Angeles area are weighted to compensate for the fact that the first set were obtained in 39 visits, the second in 34 visits, and the third in 32 visits.

In grouping entities by zone, each was assigned to high intertidal, mid-intertidal, low intertidal, or tide pools according to where it had the highest total score. In respect to geographical distribution, species were grouped into those which appear to be

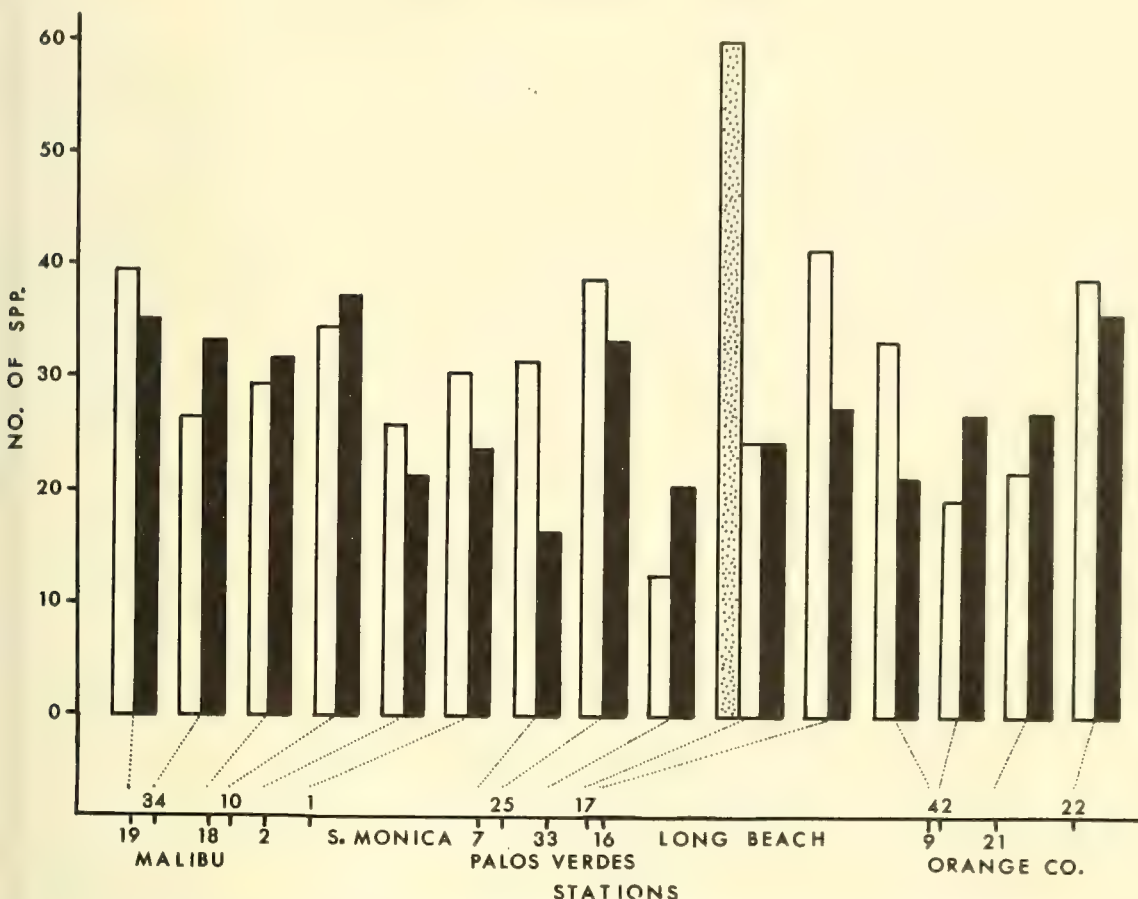


Figure 2. Overall number of species reported from stations in the Los Angeles area. Open bars: 1956-9. Solid bars: 1968-70. Stippled bar: Dawson's analysis of Setchell and Gardner's collections (1895-1912).

mainly northern forms near their southern limit in southern California, mainly southern forms near their northern limit, or cosmopolitan. A species was counted as endemic if its distribution seems to be centered on southern California and does not range outside California or Pacific Baja California. Information was mainly taken from Dawson (1961). In the classification by habit, only the articulated corallines represent a taxonomic category. The massive species are mainly kelps. The turf category was given precedence over the leafy in the case of *Ulva*, because of the characteristic habit of the most common species in southern California, *U. californica*. The leafy category includes a few brown algae as well as red. The crustose forms include encrusting corallines as well as *Ralfsia* and encrusting non-coralline red algae. A few species are found characteristically coming up through sand while firmly attached to rocks buried in the sand. This habit seems to be distinct from that of the great number of species which are occasionally found

half buried by rising sand levels. The determination of the month of maximum occurrence of entities is discussed below (p. 10). The assignment of each entity in these various categories is given in Table I.

Total scores by station. — In Figure 5, the total scores for each station in the Los Angeles area in 1968-70 are compared with the scores for the years 1956-9. In the case of stations visited more than once, the arithmetic mean is used. The standard deviation between different total scores for the same station is 40 for the 1968-70 observations and 35 for the 1956-9 ones.

Before using the arithmetic mean of multiple observations for Figure 5, I needed to investigate the possibility that there are systematic seasonal variations in the score at any one station. This problem was made difficult by the fact that Dawson's work shows a strong bias with respect to the seasons of January-March, April-June, July-September, and October-December (1959a, Tables I and II). He made very few visits during the summer

and very few visits to the same station during the same season in a different year.

The sign test for the paired case (Alder and Roessler, 1964: 150) was used to test for the presence of systematic seasonal variation in the total scores at each station. In this statistic, all the repeated visits made by Dawson to the same station at different seasons were classified by the season of the earlier and the later visit. Thus all the differences between the pairs of same station-different season visits were grouped over all stations as Spring-Summer, Spring-Autumn, Spring-Winter, Summer-

Autumn, Summer-Winter, and Autumn-Winter differences. The positive or negative sign of these differences was determined, and a greater than random preponderance of a particular sign would indicate the presence of a systematic variation, although it would not determine its size.

No systematic variation could be detected by the sign test at the 5% level of significance. Moreover, the 1968-70 visits were found to have much the same bias against summer observations as did the 1956-9 study. So it was thought safe to use the arithmetic mean for the values shown in Figure 5.

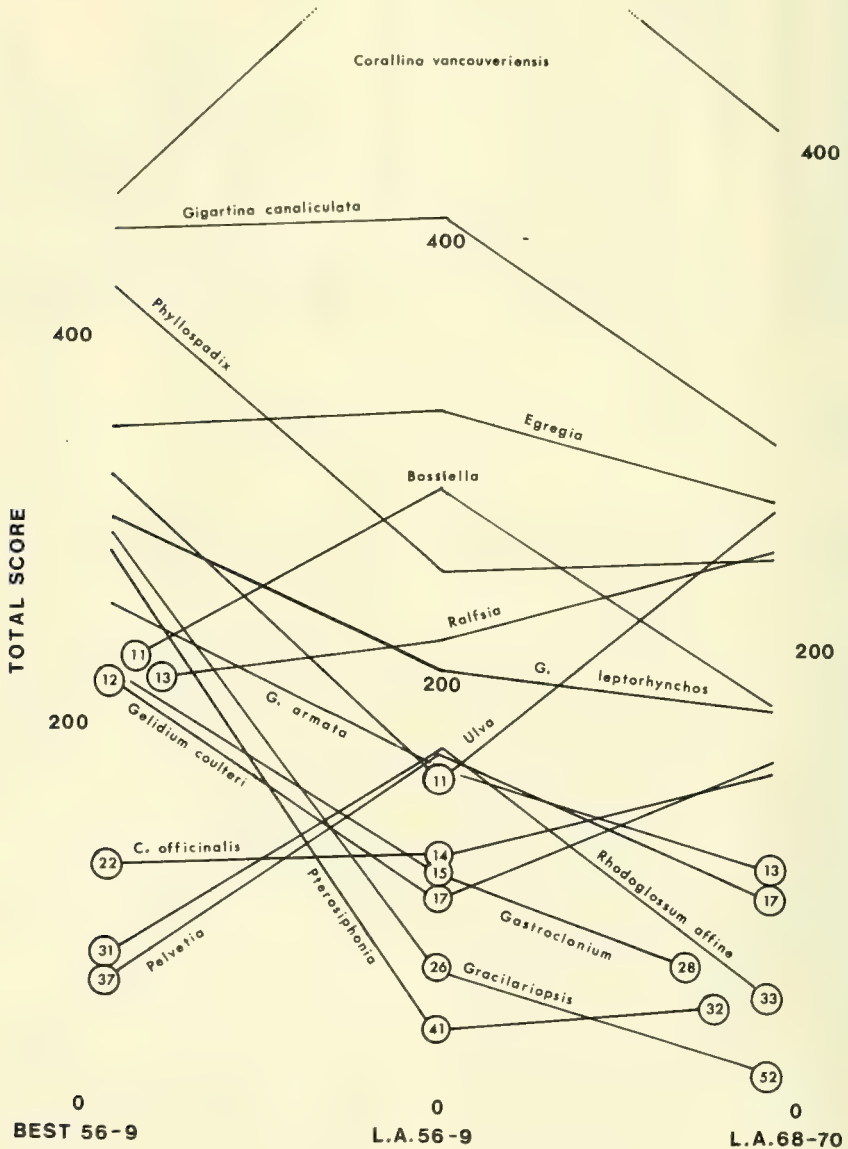


Figure 3. Total scores for the most common species (or groups of species) compared for the original southern California flora (as indicated by Dawson's best 15 stations outside the Los Angeles area), the 15 Los Angeles stations 1956-9, and the same stations 1968-70.

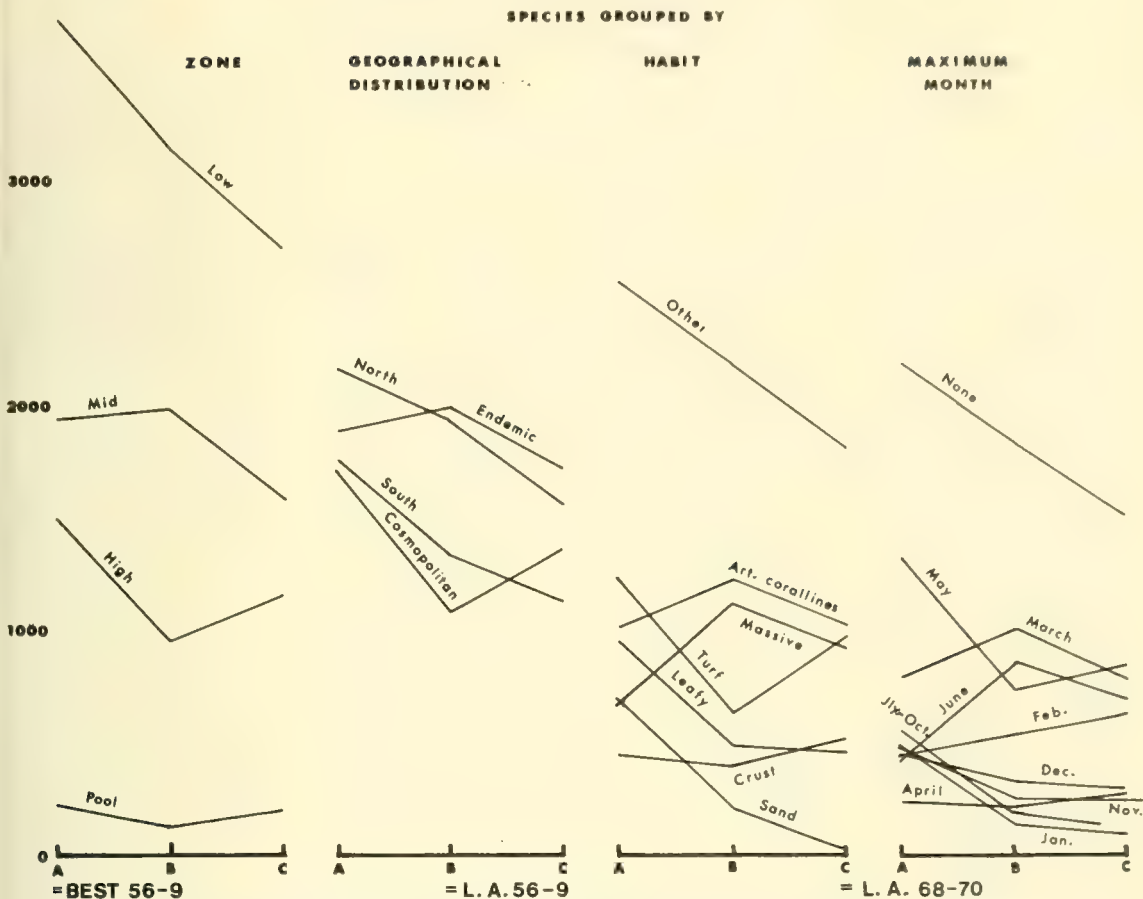


Figure 4. Total scores for various non-taxonomic groups of species compared for: A — Dawson's 15 best stations outside the Los Angeles area; B — the 15 stations in the Los Angeles area in the period 1956-9; and C — the same stations as B in the period 1968-70.

Seasonal variations — Nevertheless, I have the subjective impression that conspicuous seasonal variations, at least in quantity, do occur in the algal flora, with a maximum in late spring and a minimum in late summer. There are three possible ways in which such a variation could exist and not appear in the test. First, shifting sand appears to be the major factor in variation (Dawson, 1965a: 225). If this shifting is random with regard to season at any one station, it could obscure seasonal variation. Second, the period of any variation, or differences from year to year in the time at which peaks occur, could be such that Dawson's division of the year into four seasons would not be precise enough to detect seasonal variation. Third, a summer flora of small species could replace a winter flora of large species, so that the number of species remains much the same while the total bulk of algae changes from season to season.

These possibilities were tested by an investigation

of the total scores given each entity for each month (Fig. 6). Data were used from all Dawson's station visits throughout southern California, and from the first visit made to each station in the present study. (It was thought that the inclusion of the second and third visits made in the present study would bias the data too much in favor of stations in the Los Angeles area). The distribution of station visits by month in the data used was found to range from 20 in November and 18 in January and February, to 2 in August and 4 in July and September. Data from the earlier visit in August were added to those in July to make a 'month' of 50 days with 5 visits, and the later August visit was added to those in September to make a month of 40 days with 5 visits also. The score for each species in each month was then weighted by a ratio of 20 to the number of visits made in each particular month. Running means of three months were used to smooth the weighted data of each species. The

TABLE I. Scores and classification given each species
(or other taxonomic category).

SPECIES OR ENTITY	SCORE		LEVEL	CLASSIFICATION ACCORDING TO:		
	1956-9	1968-70		DISTRIB.	HABIT	MAX. MONTH
<i>Corallina vancouveriensis</i> /						
<i>gracilis</i>	568	420	MID	North	Art. coral.	MAR.
<i>Gigartina canaliculata</i>	401	285	MID	Endemic	Other	NONE
<i>Egregia laevigata</i>	332	260	LOW	South	Massive	NONE
<i>Bossiella</i> spp.	280	174	LOW	North	Art. coral.	NONE
<i>Phyllospadix</i> spp.	244	238	LOW	North	Other	NONE
<i>Ralfsia</i> spp.	205	241	HIGH	Cosmop.	Crust.	DEC.
<i>Gigartina leptorhynchos</i>	199	173	MID	Endemic	Other	NOV.
<i>Rhodoglossum affine</i>	162	45	MID	North	Other	JUNE
<i>Pelvetia fastigiata</i>	159	91	MID	Endemic	Massive	JUNE
<i>Gigartina armata</i> /spinosa	154	104	LOW	Endemic	Massive	FEB.
<i>Ulva</i> spp.	152	257	HIGH	Cosmop.	Turf	MAY
<i>Pterocladia pyramidale</i>	137	94	LOW	South	Other	MAR.
<i>Pachydictyon coriaceum</i>	114	100	LOW	South	Leafy	JUNE
<i>Corallina officinalis</i> var.						
<i>chilensis</i> /pinnatifolia	114	144	LOW	Cosmop.	Art. Coral.	APR.
<i>Gastroclonium coulteri</i>	111	48	LOW	North	Other	NONE
<i>Lithothrix aspergillum</i>	97	81	LOW	Endemic	Art. Coral.	MAR.
<i>Gelidium crinale</i> /coulteri	94	150	HIGH	South	Turf	NONE
<i>Gelidium pulchrum</i> /purpurescens	93	44	LOW	Endemic	Other	JUNE
<i>Eisenia arborea</i>	91	83	LOW	Endemic	Massive	MAY
<i>Prionitis lanceolata</i>	87	114	LOW	Endemic	Massive	FEB.
<i>Enteromorpha</i> spp.	76	83	HIGH	Cosmop.	Turf	MAY
<i>Ceramium</i> spp.	70	23	MID	Cosmop.	Turf	MAY
<i>Gelidium robustum</i>	66	109	LOW	Endemic	Other	FEB.
<i>Chaetomorpha aerea</i>	66	10	HIGH	Cosmop.	Sand	NONE
<i>Laurencia pacifica</i>	66	88	LOW	Endemic	Other	NONE
<i>Gracilaria</i> /Gracilariopsis spp.	63	13	LOW	South	Sand	JULY- OCT.
<i>Melobesia mediocris</i>	63	102	LOW	North	Crust.	JUNE
<i>Plocamium coccineum</i> var.						
<i>pacificum</i>	60	70	LOW	Endemic	Other	FEB.
<i>Porphyra</i> spp.	58	30	HIGH	Cosmop.	Leafy	JULY- OCT.
<i>Cryptopleura</i> spp.	58	18	LOW	North	Leafy	JAN.
<i>Halidrys dioica</i>	57	47	LOW	Endemic	Massive	JUNE
<i>Petrospongia rugosum</i>	54	20	HIGH	South	Other	MAY
<i>Cystoseira</i> spp.	52	47	LOW	Endemic	Massive	MAY
<i>Rhodymenia pacifica</i> /lobata/						
<i>palmettiformis</i>	49	69	LOW	North	Leafy	FEB.
<i>Chondria nidifica</i>	48	3	LOW	South	Sand	DEC.
<i>Centroceras clavulatum</i>	45	25	MID	South	Turf	MAY
<i>Lithophyllum</i> /Lithothamnion spp.	44	58	HIGH	Cosmop.	Crust.	JAN.
<i>Zonaria farlowii</i>	42	56	POOL	South	Other	MAY
<i>Colpomenia</i> sp.	37	73	MID	South	Other	JUNE
<i>Gymnogongrus leptophyllus</i>	36	16	MID	Endemic	Other	JUNE
<i>Pterosiphonia</i> spp.	36	46	MID	Cosmop.	Turf	FEB.
<i>Ectocarpus</i> /Giffordia spp.	34	48	POOL	Cosmop.	Turf	APR.
<i>Acrosorium uncinatum</i>	33	9	LOW	South	Leafy	MAR.
<i>Hildenbrandia</i> sp.	33	22	HIGH	Cosmop.	Crust.	MAR.
<i>Smithora naiadum</i>	30	72	LOW	North	Leaf	MAY
<i>Gigartina papillata</i> /cristata	25	37	HIGH	North	Other	JULY- OCT.

TABLE I (CONTINUED). Scores and classification given each species
(or other taxonomic category).

SPECIES OR ENTITY	SCORE		LEVEL	CLASSIFICATION ACCORDING TO:		
	1956-9	1968-70		DISTRIB.	HABIT	MAX. MONTH.
<i>Prionitis cornea/australis</i>	27	12	LOW	Endemic	Other	—
<i>Dictyopteris zonarioides</i>	24	14	LOW	South	Other	APR.
<i>Macrocytis</i> sp.	24	3	LOW	North	Massive	MAR.
<i>Cladophora trichotoma</i>	24	12	HIGH	North	Other	—
<i>Spermothamnion snyderae</i>	24	21	LOW	Endemic	Turf	FEB.
<i>Dictyota flabellata</i>	22	38	POOL	South	Leafy	JUNE
<i>Laurencia splendens/diegoensis</i>	19	4	LOW	Endemic	Other	JAN.
<i>Chondria californica</i>	15	0	LOW	South	Other	DEC.
<i>Rhodymenia rhizoides</i>	16	0	LOW	Endemic	Leafy	—
<i>Sargassum agardhianum</i>	12	19	LOW	South	Massive	APR.
<i>Gymnogongrus platyphyllus</i>	12	0	LOW	North	Other	—
<i>Lophosiphonia</i> spp.	12	27	MID	Cosmop.	Turf	NOV.
<i>Chondria decipiens/pacifica</i>	12	0	LOW	Endemic	Sand	MAY
<i>Codium fragile</i>	11	11	LOW	North	Other	DEC.
Blue-green algae	10	6	—	Cosmop.	Turf	—
<i>Taonia lennebackerae</i>	9	22	POOL	South	Leafy	JUNE
<i>Scytosiphon lomentaria</i>	9	10	HIGH	Cosmop.	Other	MAY
<i>Nienburgia andersoniana</i>	9	3	LOW	Endemic	Leafy	JAN.
<i>Rhodymenia californica</i>	9	0	LOW	South	Leafy	—
<i>Hapterophycus canaliculatus</i>	9	0	—	South	Crust	—
<i>Hesperophycus harveanus</i>	6	0	HIGH	Endemic	Massive	—
<i>Endarachne binghamiae</i>	6	23	MID	South	Leafy	JULY- OCT.
<i>Calliarthron</i> spp.	6	12	LOW	North	Art. Coral.	—
<i>Anisocladella pacifica</i>	6	0	LOW	Endemic	Leafy	NONE
<i>Botryglossum farlowianum</i>	6	0	LOW	North	Leafy	—
<i>Endocladia muricata</i>	5	0	HIGH	North	Other	—
<i>Microcladia</i> spp.	4	12	LOW	North	Other	—
<i>Cruoriella</i> sp.	4	6	HIGH	South	Crust.	—
<i>Nemalion helminthoides</i>	4	5	HIGH	North	Other	—
<i>Bryopsis</i> sp.	3	1	POOL	Cosmop.	Other	—
<i>Leathesia difformis</i>	3	0	MID	North	Other	—
<i>Cladophoropsis fasciculata</i>	3	0	—	South	Turf	—
<i>Jania natalensis</i>	3	0	POOL	South	Art. Coral.	NONE
<i>Agardhiella coulteri</i>	3	0	—	Cosmop.	Other	MAY
<i>Plocamium violaceum</i>	3	0	—	North	Other	—
<i>Schizymenia</i> sp.	3	0	LOW	North	Leafy	—
<i>Grateloupia</i> spp.	3	11	LOW	Cosmop.	Leafy	NOV.
<i>Herposiphonia</i> spp.	3	43	MID	Cosmop.	Turf	—
<i>Laminaria</i> sp.	1	0	LOW	North	Massive	—
<i>Cladophora graminea</i>	1	0	—	South	Other	—
<i>Callophyllis</i> spp.	1	0	LOW	North	Leafy	—
<i>Carpopeltis bushiae</i>	1	0	—	Endemic	Other	—
Filamentous diatoms	0	25	—	Cosmop.	Turf	—
<i>Laurencia subopposita</i>	0	12	LOW	South	Other	MAR.
<i>Polysiphonia</i> spp.	0	12	MID	Cosmop.	Turf	MAY
<i>Ophidocladus californicus</i>	0	12	—	Endemic	Turf	—
<i>Pterochondria</i> sp.	0	3	—	North	Turf	—
<i>Bangia</i> sp.	0	9	HIGH	Cosmop.	Other	APR.
<i>Ulothrix</i> sp.	0	9	—	Cosmop.	Other	—

species were then grouped according to the month in which the running means showed a maximum. The species in which the maximum running mean was not more than double the value of the minimum running mean were considered to have no maximum. Then, the original weighted data, not the running means, of each species in each group were added together, and the result is shown in Figure 6.

Ranking of stations.—The changes noted in the algal flora of the various stations between 1956-9 and 1968-70 are shown in Table II. These changes were ranked in order from greatest decrease to greatest increase. The ranks based on species number and average score showed the high rank correlation coefficient (Scheffler, 1969: 133) of $+0.7$, so a combined ranking was determined using the changes in both the species number and the average score, and is shown in Table II.

The stations were also ranked according to the degree they are exposed to human use and collecting activity, to air pollution, and to marine pollution

from sewage outfalls. These are the three factors quoted by Dawson (1965a: 174, 181) as probable causes of deterioration in the algal flora. The ranking according to human use was made after a consideration of the length of walk from the nearest roadhead by public access to the station, the amount of parking available in the vicinity of the roadhead, and the degree to which the area is built up. The factors considered in the ranking according to exposure to air pollution are shown in Figure 7. The number of days per year when the measured concentration of oxidant exceeded the state ambient air quality standard was used as a measure of air pollution. All the monitoring stations, however, are far from the beach, so the ranking was derived from a consideration of the prevailing winds in the area, the distribution of high ground, and the pattern shown by the incidence of higher than standard levels of oxidant at the inland monitor stations.

The information used for ranking the intertidal

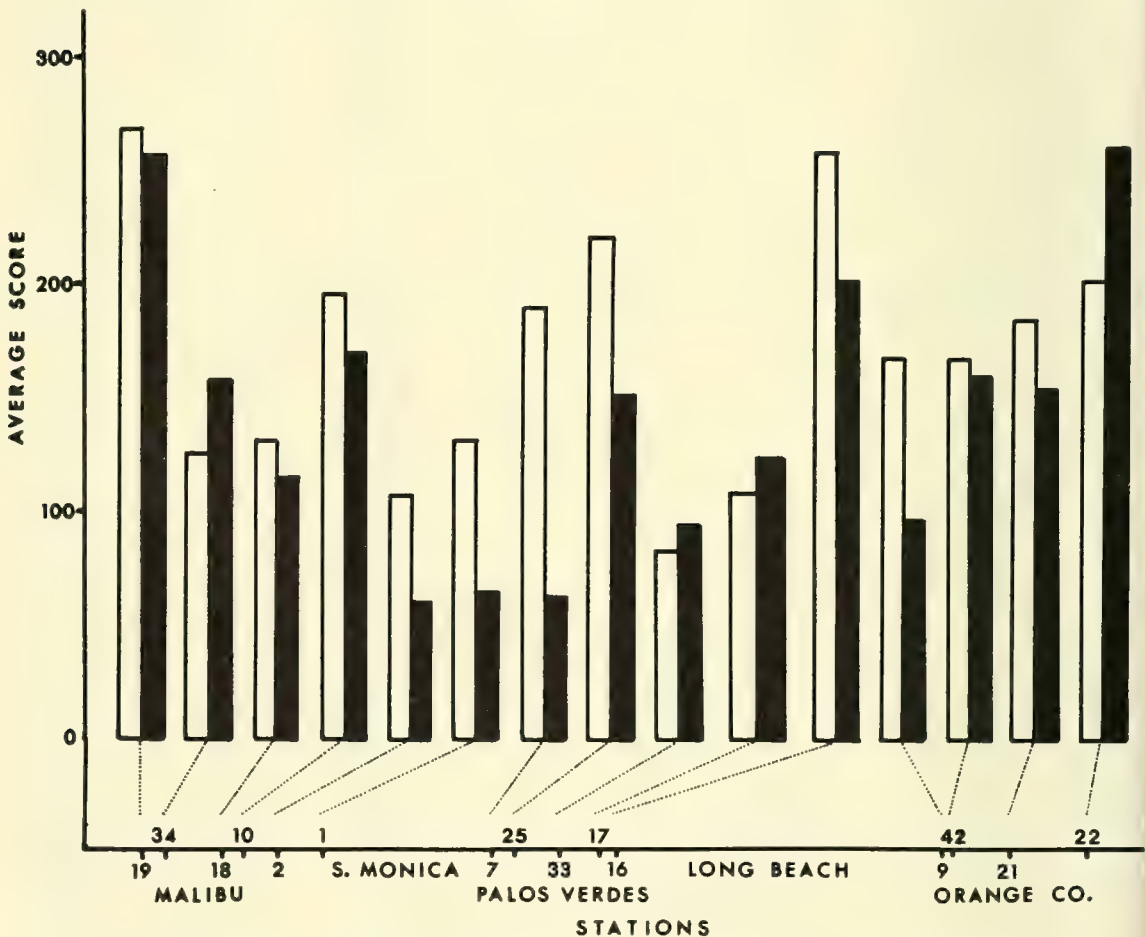


Figure 5. The average scores reported from the stations in the Los Angeles area compared for 1956-9 (open bars) and 1968-70 (solid bars).

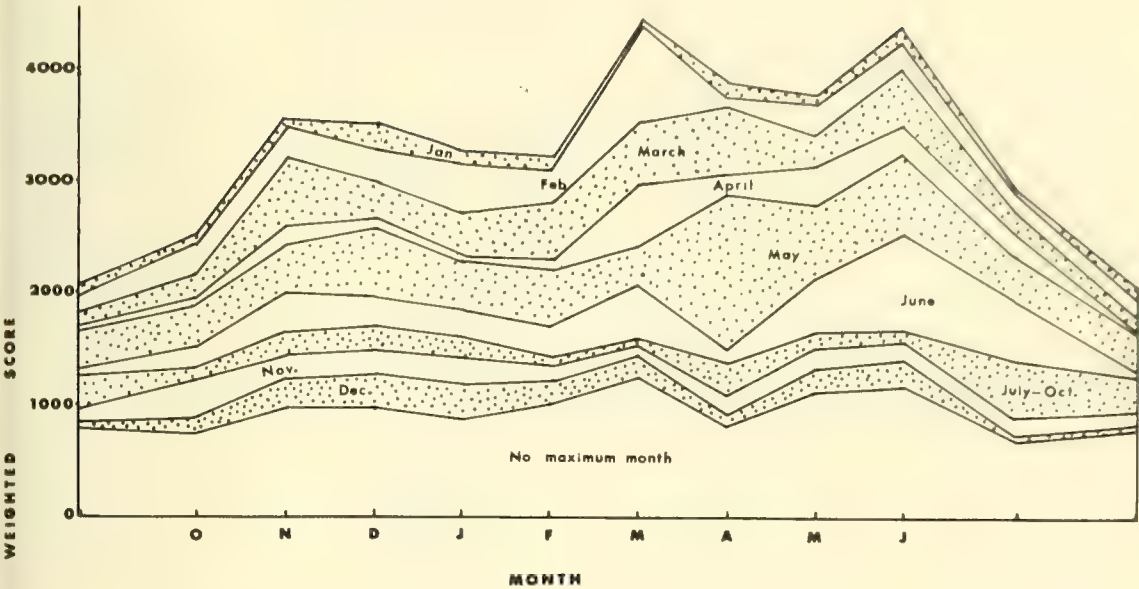


Figure 6. Seasonal variations in the intertidal flora of southern California. The top line represents the total weighted score for each month, summed for all species and all stations visited. The intermediate bands represent the contributions to this total made by all the species found to have a maximum in the month indicated (according to smoothed data, see p. 10).

stations according to the effects of marine pollution from sewage outfalls is shown in Table III and Figure 8. It may be seen from Table III that, in the case of the three largest outfalls, the increase in discharge from 1956-9 to the present is roughly proportional to the present figures, so that a ranking based on either criterion is the same. Station 21 (Laguna Beach) is ranked 15th because the outfall at this station was closed in 1959 and the new Laguna Beach outfall opened more than a mile to the southwest. Coliform bacteria counts taken recently near Station 21 are therefore much less than those found during 1956-9 (L. Burtman, personal communication).

The distribution of coliform bacteria around the three largest outfalls is shown by stippling in Figure 8. For the area around the Hyperion outfall (Calif. Reg. Water Pollution Cont. Bd. No. 4, 1965, Tables D and H) the data are tabulated as the number of analyses which showed surface water to have 10 or more MPN/ml of coliform bacteria. The dense stippling represents the area monitored by those of the 16 offshore stations which had the maximum of 2 out of 104 analyses showing 10 or more MPN/ml coliform bacteria. Among the 17 shore stations, dense stippling represents 9 to 12 cases out of 617 analyses at each station. Off White Point (Rittenberg, Mittwer, and Ivler, 1958, Fig. 3) the dense stippling represents counts of 1000 to >10000 MPN/cm² coliform bacteria in bottom sediments

obtained at certain of 106 sampling stations. Off the Orange County outfall (Rittenberg *et al.*, 1958, Fig. 1) dense stippling represents counts of 3000 to >12000 MPN/cm² coliform bacteria in bottom sediments obtained at certain of 100 sampling stations. In all these cases, the boundary of the area sampled is shown by a broken line, and the sampling stations are fairly evenly distributed within that area.

Thus, the available measurements from the Hyperion outfall are not strictly comparable to

TABLE III. Average dry weather discharge of sewage outfalls in area studied (millions of gallons per day).

OUTFALL	1957-9 ^a	1969	INCREMENT
Dana Point	0.1	1.0 ^b	+ 0.9
South Laguna	0.6	0.5 ^b	- 0.1
Laguna Beach	1.0	2.0 ^b	+ 1
Orange County	55.0	119 ^c	+ 64
White's Point (3)	277.0	360 ^d	+ 83
Hyperion (effluent)	275.0	340 ^d	+ 65
Hyperion (sludge)	3.6	4.0 ^d	

^aAllan Hancock Foundation, 1965, Table 1.1.
^bBurtman, pers. comm.
^cBueermann, pers. comm. (data for period 1967-9).
^dHertel, pers. comm.

TABLE II. Description of intertidal sampling stations.

STAT. NO.	GEOGRAPHICAL NAME	CHANGE	% CHANGE	RANK ACCORDING TO MAXIMUM:				NO. VISITS	
		IN NO. OF SPP.	IN AV. SCORE	DECREASE	USE	SEWAGE	OXIDANT	1956-9	1968-70
19	Latigo Shore Rd.	-4	-4%	7	12	13	8	3	2
34	Malibu Shore Rd.	+7	+18%	14	8	12	7	2	2
18	Malibu Beach	+2	-12%	9	11	11	4	3	2
10	Big Rock Beach	+3	-15%	10	9	10	3	2	2
2	Topanga Canyon	-4	-44%	5	10	9	2	3	2
1	Sunset Blvd.	-7	-48%	2	1	8	1	4	2
7	Flat Rock Pt.	-15	-40%	1	6	5	5	1	2
25	Lunada Bay	-5	-32%	6	7	4	6	3	3
33	Portuguese Pt.	+8	+17%	15	15	2	11	1	2
17	White Pt.	0	+16%	11	3	1	10	3	2
16	Pt. Fermin								
	(Cabrillo Beach)	-14	-23%	4	4	3	9	2	2
9	(Little) Corona								
	del Mar	-12	-43%	3	5	6	12	2	2
42	Crystal Cove	+8	-3%	13	13	7	13	1	2
21	Laguna Beach	+6	-16%	8	2	15	14	2	2
22	Dana Point North								
	(Salt Creek)	-2	+31%	12	14	14	15	2	3

those published about the White Point and Orange County outfalls, while the latter two are seriously out of date. Moreover, differences in sewage treatment (continuous chlorination is performed at Hyperion but not at White Point) affects the incidence of coliform bacteria but may not affect other deleterious components of sewage. Indeed, it is possible that chlorine itself is harmful to algae. However, the data presented seem sufficient to establish a ranking system for the stations occupied.

The ranks assigned to each intertidal station according to each factor is shown in Table II.

RESULTS AND DISCUSSION

The reduction in the marine intertidal flora near Los Angeles since 1956-9 is general and widespread. Figures 2 and 5 show a very similar situation from station to station even though they illustrate two different aspects; the diversity and the quantity of the flora. Almost all of the more frequent species shown in Figure 3 and the more general groupings shown in Figure 4 show a downward trend.

In Figures 3 and 4, data from the best stations outside the Los Angeles area are used as an indication of what the southern Californian flora may have been before the effects of human activity became apparent. While there is an obvious downward trend from the best stations through the Los Angeles stations in 1956-9 to the latter in 1968-70, in many individual species and groups of species

the pattern of change is not consistent. Although the 'best' stations (different localities from the Los Angeles stations) might make the data for rare species or small groups incomparable, the total scores for the common species and the larger groups should be more consistent than shown. Thus, it is probable that the factor responsible for the decline before 1956-9 is different from that responsible for the decline after this period. There seems no reason to doubt Dawson's conclusion that the major factor in the deterioration prior to 1956 was marine pollution from sewage outfalls.

Those entities which show a consistent decrease include *Gigartina leptorhynchos*, *Gigartina armata*/*spinosa*, *Gastroclonium*, and *Gracilaria*/*Gracilariaopsis*. Similar species groups include the four largest groups; the low intertidal, the northern, those of miscellaneous habit, and those without a maximum month which tends to confirm the suggestion that the decrease is very general. The group showing the most dramatic decline is that which includes those entities which characteristically are found growing up through sand. These species seem to be relatively well protected from collectors. Perhaps the sand provides a mechanism by which pollutants are held in more effective contact with the plant than is the case with other habitats. On the other hand, these plants could be declining simply because their habitat is being reduced by the erosion of sandy beaches. The southern entities show much the same consistent decline as the

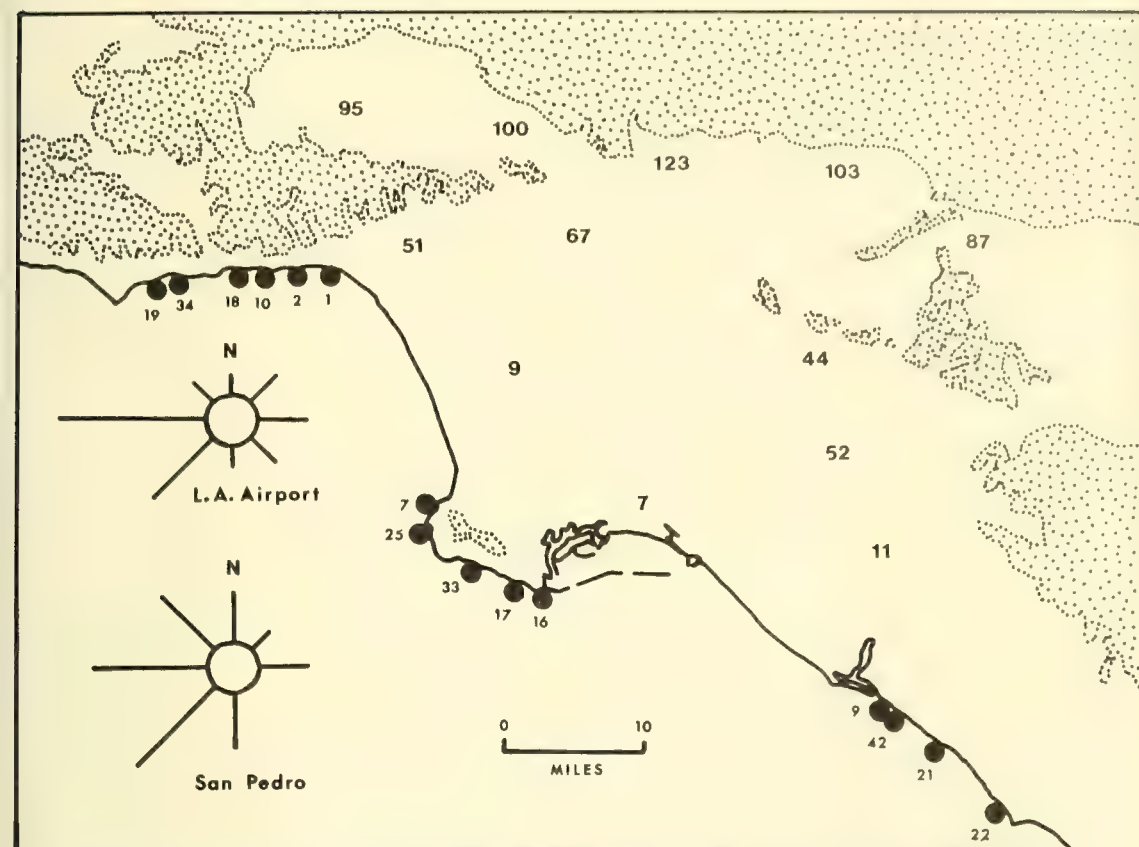


Figure 7. The information used to determine the ranking of intertidal stations (solid circles, small numerals) according to the amount of air pollution. (Stippled area: land over 1000 feet elevation; large numerals: number of days oxidant exceeded California State standards in the year 1968-9 [Calif. Air Res. Bd. 1969a, b, c, d.]; wind roses: the prevailing winds at Los Angeles Airport [U. S. Weather Bur., 1962, p. 15] and San Pedro [Stevenson, 1959, Fig. 9B]).

northern; they might perhaps be expected to increase if thermal pollution were an important factor. The decline of leafy forms was mentioned by Dawson. In the groupings by maximum month, those with maxima in the summer, fall, and early winter (July to January) show a consistent decline.

Those entities which show an inconsistent pattern of decline before 1956 and an increase after include *Ulva*, *Gelidium crinale*/*coulteri*, and *Pterosiphonia* spp. The main feature these plants have in common is a turfy habit, which is particularly protected from collectors (as is also the crustose habit). The presence of *Ulva* and *Gelidium crinale*/*coulteri* in the high intertidal category, and *Ulva* in the cosmopolitan and May maximum groups is mainly responsible for the similar appearance of the trend in these groups.

Those species which show an inconsistent pattern of increase before 1956-9 and a decrease after include *Corallina vancouveriensis*/*gracilis*, *Bos-siella* spp., *Rhodoglossum affine*, and *Pelvetia*. The

first two are articulated corallines which Dawson mentioned particularly as being favored by sewage pollution. *Rhodoglossum affine* and *Pelvetia*, as well as *Corallina vancouveriensis*, contribute to the similar pattern shown by mid-intertidal forms, which are especially vulnerable to both collection and air pollution. *Corallina vancouveriensis*/*gracilis* has a similar effect on the March group, while both *Pelvetia* and *Rhodoglossum affine* have a maximum in June.

Finally, a small consistent increase is shown by *Ralfsia*, *Corallina officinalis* var. *chilensis*, and species with a maximum month in February. In the latter case, no one species appears to be responsible for the effect.

No quantitative measurements are available for most of the stations with respect to human use, air pollution, or water pollution. In addition, these factors are complex in themselves, and may operate on any particular species indirectly, through their effect on another species which has an effect on the

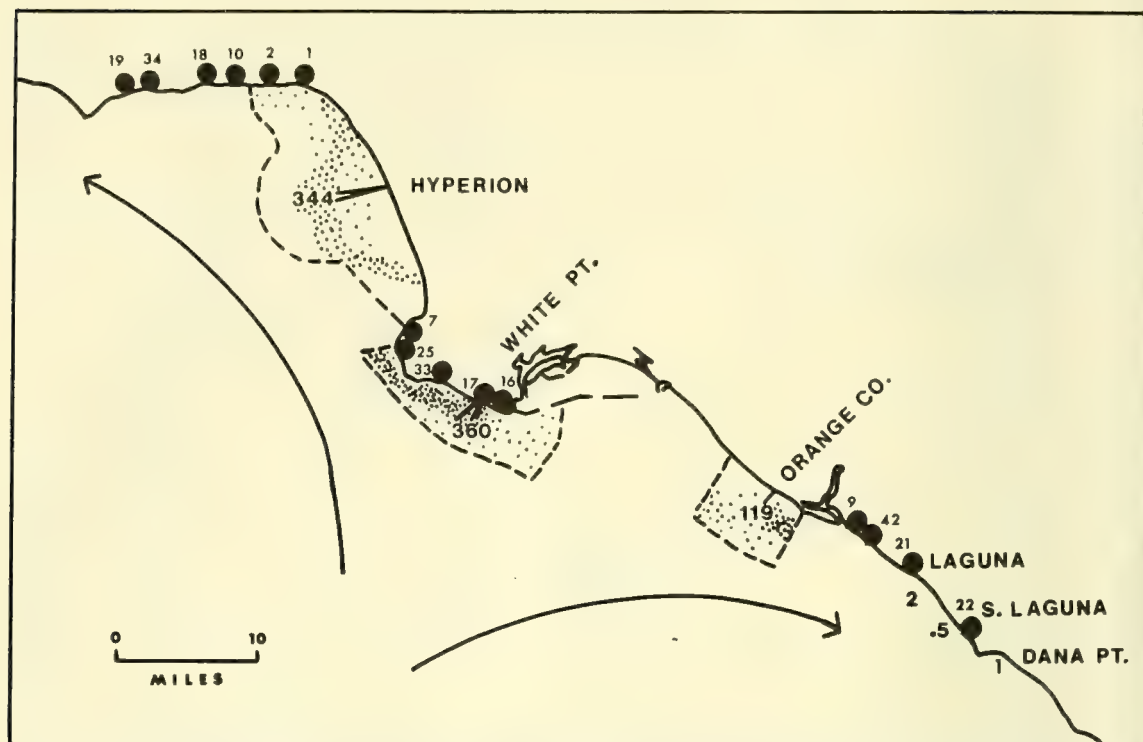


Figure 8. The information used to determine the ranking of intertidal stations (solid circles, small numerals) according to pollution from sewage outfalls (named). (Large numerals: MGD. average dry weather discharge [see Table III]; stippled areas: distribution of coliform bacteria [see text, p. 11]; arrows: general off-shore ocean currents [Emery, 1960, Fig. 87]).

species in question, rather than directly. At the present stage of knowledge, non-parametric statistics are the best that can be used. Rank correlation coefficients were calculated between the rank for the change in the flora at each station between 1956-9 and 1968-70, and the rank assigned each station with respect to human use, air pollution, and sewage pollution. These coefficients are +0.6, +0.4, and +0.2 respectively.

Thus, of the main factors suggested for the decline of the algal flora, the most important since 1956-9 are: first, human use; second, air pollution; and third, pollution from sewage outfalls. This is in contrast with the decline up to 1956 where, as has been said above, there is no reason to doubt Dawson's conclusion that sewage pollution was the major factor.

Even without a statistical analysis, it is obvious that there are some stations which are particularly high in one factor and low in others. Station 9 (Little Corona) seems to have little air and water pollution, but it is a favorite spot for collectors. It has shown a drastic decrease in algae. It remains to be seen whether it will recover now that it has been made a marine preserve. Station 42 (Crystal Cove) is difficult of access but is close to Station 9 and

presumably shares with it much the same level of air and water pollution; the flora there has improved. Station 33 (Portuguese Point) is totally shut off from the public, while it suffers a high degree of sewage pollution; the flora there has improved, although it is still at a low level. Station 2 (Topanga Canyon Rd.) suffers heavy air pollution, is difficult of access, and has at most moderate sewage pollution; the flora there has obviously decreased.

The data shown in Figure 6 indicate that there is indeed much seasonal variation in the algal flora of southern California, with a maximum in March-June and a minimum in August-September. Most of this variation is the effect of variation in species which are present throughout the year. Year to year variations probably make the grouping of observations by season unreliable but, if this is to be done, it would be better to divide the year into three four-month seasons: November-February; March-June; and July-October. There seems to be no justification for Dawson's statement first (1965a: 224) that "In gross aspect the southern California benthic algal flora does not show conspicuous seasonal differences in quantity or quality," and second (1965a: 225) that "At most stations the flora as a whole shows a decline in growth and

luxuriance during the winter and spring and an increase during the summer and fall."

CONCLUSIONS

The main purpose of an exploratory study such as the present one is to suggest the direction of future work. It is obviously desirable that the present non-parametric methods should be replaced by more precise quantitative ones. Practical considerations demand that a more precise study should be a more restricted one.

Future work could be concentrated on certain species over wider areas than the stations sampled, or on the entire flora of certain areas more detailed than the present stations. Small areas studied in detail are extremely vulnerable to the effects of sand movement and man-made changes of substratum (such as the building of a jetty across the transect line of Station 1). These factors are part of the scene, and no attempt was made to exclude them in the present general study, but they are difficult to evaluate in terms of 'pollution'. Studies of certain particular species over a wide area would be less vulnerable to such factors and also make them easier to evaluate. In conjunction with experimental work, the distribution of these species might be related to certain specific pollutants, and so make them valuable as indicator organisms.

Grouping species into taxonomically heterogeneous categories (Fig. 4) did not produce much information, except that plants coming up through sand appear to be particularly vulnerable. So, the entities chosen for detailed study should be the smallest taxonomic unit readily identifiable in the field. The use of taxonomic units which require identification in the laboratory would require extensive collections which would be undesirable in principle and would add greatly to the work needed for the study. (An exception would be needed in the case of many turf forming genera).

The choice of species to be studied must also take into account seasonal variations (Fig. 6). If the study could not be carried on throughout the year, the species could be chosen which have only a slight seasonal variation (Table I). However, since most probable pollutants also have seasonal fluctuations in their occurrence, it would be much more desirable to monitor both species and pollutant throughout the year. Frequent observations would also be needed to suggest when dying and damaged plants could be showing the effects of pollution and when they are simply the effects of drying winds.

It would also be advisable to use species which appear to have decreased in response to pollution,

rather than those which have increased, since there are so few of the latter.

Gastroclonium coulteri and *Chaetomorpha aerea* are two species which are easily identified, have little seasonal variation, and have shown a consistent decline both before 1956 and after. Their decline could perhaps be used as a general measure of 'pollution'.

Rhodoglossum affine, *Bossiella* spp., *Pelvetia fastigiata*, *Gigartina armata/spinosa*, and *Gelidium pulchrum/purpurescens* all have shown a relatively great decrease since 1956-9 and presumably are sensitive to the factors which are causing a decline in the intertidal flora at the present time. However, all except *Bossiella* show a marked seasonal variation, and all except *Rhodoglossum* and *Pelvetia* contain more than one recognized taxonomic species.

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A NEW SPECIES OF *SIMOPELTA* FROM COSTA RICA (Hymenoptera: Formicidae)

ROY R. SNELLING¹

ABSTRACT: *Simopelta paeminosa*, new species, is described from Puntarenas Province, Costa Rica. Diagnostic features of this species are: tridentate mandibles with acute basal tooth; no median clypeal spine; rugose cephalic and alitrunk integument. This species appears to be most closely allied to *S. williamsi* of Ecuador.

The ponerine genus *Simopelta* was reviewed by Gotwald and Brown (1966), who discussed the generic characters, listed the known species and

described two new species. They also published

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observations on the behavior of *S. oculata* Gotwald and Brown made by Brown in Costa Rica. These observations reaffirmed the army antlike behavior of the foraging workers.

The following new species from Costa Rica was included in a vial containing three workers, two males and one mangled larva of *Gnamptogenys simplex* (Emery). The two males are not fully colored and one has the wings torn off on one side. It seems likely that the *Gnamptogenys* represent the prey of the *Simopelta*; unfortunately, the collector after three years, was unable to recall details of the collection.

***Simopelta paeminosa*, new species**

Figure 1

Diagnosis. Clypeus without median spine; eyes small; mandibles tridentate, basal tooth acute; head, alitrunk and petiole coarsely rugose; integument blackish brown.

Holotype worker: TL 4.1; HL (occipital margin to anterior border of frontal lobes) 0.9; HW (without eyes) 0.7; WL 1.5; greatest diameter of eye 0.06; scape L (chord, without basal neck) 0.8 mm; CI 81. Abbreviations and measurements as in Brown (1958).

Similar to worker of *S. williamsi* but differing as follows:

1. Mandibles more slender, the basal tooth acute.
2. Antennal scapes longer; in full face view, extending beyond occipital margin by about twice the apical breadth.
3. Petiolar node longer, about as high as long.
4. Rugulae of head and alitrunk not transversely oriented. In *S. williamsi*, those of the occiput and pronotum, especially, are decidedly transverse; in *S. paeminosa* the rugulae are very irregular, mostly oblique, though a few may be partially or wholly transverse. The gaster is shiny, with well separated distinct punctures.

Paratype series. Variation in ten randomly selected individuals, but including apparently largest and smallest specimens: TL 3.8-4.2; HL 0.90-0.95; HW 0.70-0.73; ML 0.43-0.50; WL 1.40-1.50 mm; CI 71-81.

Color, basically blackish brown, mandibles, flagellum, legs brownish. Pronotum with brownish areas of irregular extent. Gastric apex light brownish.

Holotype and 21 paratype workers, 4 mi south of San Vito de Java, Puntarenas Province, Costa

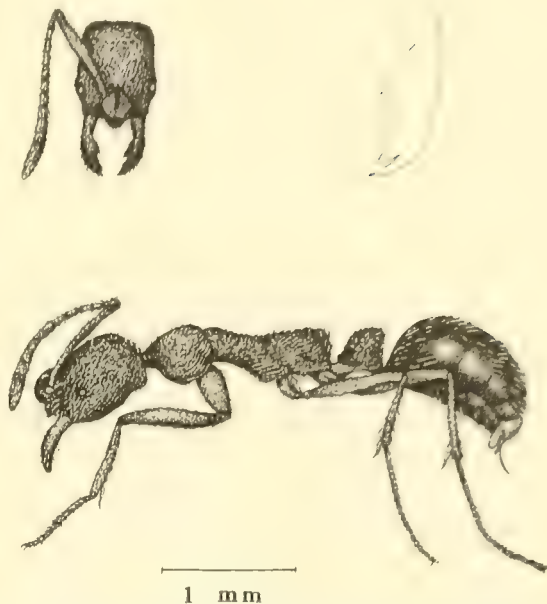


Figure 1. *Simopelta paeminosa*, new species. Above, head in frontal view and enlarged outline of mandible. Below, lateral aspect. Figures by Ruth Ann DeNicola.

Rica, 15 August 1967 (R. W. McDiarmid). Holotype and most paratypes in the Natural History Museum of Los Angeles County. Paratypes deposited in American Museum of Natural History and Museum of Comparative Zoology.

Etymology. *Paeminosus*, L., rough or uneven, in allusion to the roughened integument.

The rugose integument of this species seems to indicate a relationship to *S. williamsi*. That Ecuadorian species, however, has the rugulae transverse on the occiput and dorsum of the alitrunk. In *S. williamsi*, too, the basal tooth of the mandible is truncate rather than acute.

In the key to *Simopelta* workers by Godwald and Brown, *S. paeminosa* fails at couplet 5 since it does not accord with either alternative. The other Central American species are punctate rather than rugulose.

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A REVISION OF THE GENUS *LOANDALIA* MONRO
WITH DESCRIPTION OF A NEW GENUS AND SPECIES OF PILARGIID POLYCHAETE¹RAYMOND R. EMERSON² AND KRISTIAN FAUCHALD²

ABSTRACT: A re-examination of the genotype of *Loandalia*, *L. aberrans* Monro (1936) demonstrated several unique morphological features not previously noted. A new genus, *Parandalia*, is established to contain the other species usually considered in *Loandalia*. Type species is *Parandalia ocularis*, new species; others include *P. americana*, *P. fauveli*, *P. gracilis* and *P. indica*.

During the examination of some polychaetous annelids from the Santa Barbara Channel, California taken in connection with a study of oil spill, January 1969, a new species of a pilargiid polychaete was recognized. It became apparent that the genus *Loandalia* Monro (1936) as presently accepted (Pettibone, 1966) contained two different groups of species. The holotype of *Loandalia aberrans* Monro (1936), which is the genotype, was borrowed from the British Museum (Natural History) and re-examined. As a consequence of these studies it was found that *Loandalia* can be accepted only as a monotypic genus; all the species presently included in that genus are here removed to a new genus, *Parandalia*.

The possibility that *Talehsapia* Fauvel (1932) could be a valid generic name for these species was considered and discarded. *Talehsapia* differs from all known pilargiids in the presence of jaws. Further, prostomial features do not resemble the pilargiids as presently accepted. *Talehsapia* is here considered *incertae sedis* and is not accepted as a valid genus in the family Pilargiidae.

Ancistargis Jones (1961) was considered a synonym of *Ancistrostylis* McIntosh (1879) by Pettibone (1966). A median antenna is present in *Ancistrostylis* and absent in *Ancistargis*. The median antenna is often difficult to detect in species of *Ancistrostylis* as remarked by Pettibone, but the character is here considered to be of sufficient importance to warrant maintaining the generic status of *Ancistargis*.

The family includes nine genera; *Ancistargis* Jones (1961) from Gulf of Mexico, *Ancistrostylis* McIntosh (1879) from Greenland, *Cabira* Webster (1879), *sensu* Pettibone (1966), *Loandalia* Monro (1936) off Angola, Africa, *Otopsis* Ditlevsen (1917) from near Iceland, *Parandalia*, new genus, *Pilargis* Saint-Joseph (1899) from France, *Sigambra* Müller (1858) from Brazil and *Synelmis* Chamberlin (1919) from the south Pacific Ocean.

The holotype and paratype specimens of the

new species have been deposited in the collection of the Allan Hancock Foundation.

Key to Genera of Pilargiidae

1. Notopodia with stout emergent hooks or spines 2.
Notopodia without emergent hooks or spines 7.
2. Notopodia with recurved emergent hooks 3.
Notopodia with stout, straight spines 6.
3. Peristomium dorsally entire *Ancistargis*
Peristomium dorsally incised 4.
4. Dorsal and ventral cirri reduced or absent; parapodia reduced, body subcylindrical *Cabira*
Dorsal and ventral cirri well developed, parapodia well developed, body dorso-ventrally flattened 5.
5. Antennae shorter than palps; integument papillated *Ancistrostylis*
Antennae longer than palps; integument smooth *Sigambra*
6. Prostomial antennae and peristomial cirri present, parapodia sharply set off from the body *Synelmis*
Prostomial antennae and peristomial cirri absent, parapodia distinct, but not set off from the body *Parandalia*
7. Prostomial antennae and peristomial cirri absent *Loandalia*
Prostomial antennae and peristomial cirri present 8.
8. Prostomium with two antennae, biarticulate palps present *Pilargis*
Prostomium with three antennae, palps without palpostyles *Otopsis*

¹Contribution from the Allan Hancock Foundation.

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Parandalia, new genus

Type species: *Parandalia ocularis*, new species.

The anterior part of the body is somewhat inflated; median and posterior parts of the body are cylindrical. A pair of eyes may be present on the anteriormost segments.

The small prostomium is indistinct; a pair of well developed, biarticulate palps with button-shaped palpostyles is present. The peristomium is separated from the prostomium by a shallow, indistinct segmental groove. Peristomial cirri are absent. The proboscis is cylindrical when everted and may terminate with several sensory papillae. The proximal surface of the proboscis is smooth.

The first parapodia are uniramous, further back all parapodia are biramous. A thick, stout, straight, crystal-clear spine emerges from the median and posterior notopodia. All notopodia are poorly developed and have at most one or two capillary setae in addition to the spine. Neuropodia where fully developed, are slightly tapering with blunt, evenly rounded tips. Dorsal cirri are absent; ventral cirri are present as small, papillar lobes. Branchiae are absent.

The neuropodia have several geniculate, pointed, simple setae. Each seta has a cylindrical stalk and a blade provided with numerous transverse rows of slender teeth.

The pygidium is an anal plaque which may have one to several short, blunt anal cirri.

Parandalia as defined above includes all species previously assigned to *Loandalia* with the exception of the type species of the latter genus. A re-examination of the type specimen of *Loandalia aberrans* Monro (1936) showed that notopodial spines are absent and that branchiae are well developed in the posterior part of the body. In addition, the two first neuropodia have thick, black acicula; a feature not found in any other described pilargiid. The species presently assigned to *Parandalia* include: *P. americana* (Hartman, 1947); *P. gracilis* (Hartman-Schröder, 1959); *P. fauveli* (Berkeley and Berkeley, 1941); *P. indica* (Thomas, 1963); and the genotype, *P. ocularis*, new species.

The different species in the genus can be differentiated as indicated in the key below and in the discussion of *P. ocularis*, new species.

Key to Species of *Parandalia*

- 1. All parapodia biramous 2.
Anteriormost parapodia uniramous,
all others biramous 3.
- 2. A single notopodial seta present;
four-five neuropodial setae present ... *P. gracilis*
Two notopodial setae present; four-twelve
neuropodial setae present *P. indica*

- 3. Eyes present; six-seven neuropodial
setae in each parapodium *P. ocularis*
Eyes absent; twelve-fifteen neuropodial
setae in each parapodium 4.
- 4. Emergent notopodial spine from
setiger 2 *P. americana*
Emergent notopodial spine from
setiger 7 *P. fauveli*

Parandalia ocularis, new species

Material examined: AHF VELERO 12856, April 3, 1969, 34°23'12"N, 119°38'18"W, 24 fms silty-clay, gear: Campbell grab, paratype (1). AHF VELERO 12860, April 3, 1969, 34°22'58"N, 119°38'05"W, 23 fms, silty-clay, gear: Campbell grab, HOLOTYPE. AHF VELERO 12864, April 4, 1969, 34°21'15"N, 119°38'00"W, 25 fms. coarse sand, gear: Campbell grab, paratype (1).

Description: Three complete individuals were collected. Length of the holotype specimen is 41 mm. Width in the widest region at the third or fourth setiger is 0.5 mm without parapodia which are poorly developed in the anterior segments. Posterior to the inflated region at about setiger 20 the width is 0.4 mm without and 0.6 mm with parapodia. The number of segments is 93.

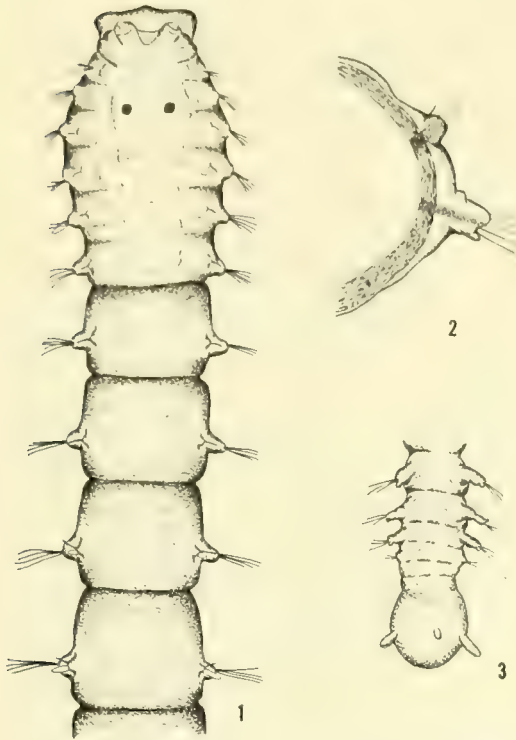
The body is a pearly white with some evidence of reddish brown colored patches on a few segments primarily near the parapodial lobes. Sections of an annulated skelopodium (chitinized secretion) cover some of the posterior segments producing a continuous reddish brown appearance. The body is cylindrical, the anterior region through the first 6 setigers is areolated and slightly dorsolaterally flattened. A pair of conspicuous, subcutaneous eyes is present on the dorsal surface between the second and third setiger. Each eye is subcircular, indicating the possible presence of a lens (Fig. 1).

The small prostomium is inconspicuous and has a pair of biarticulate palps. Each palp has a palpophore tipped with a single minute knoblike palpostyle. The palps are directed dorsally, an effect which may be somewhat accentuated by the partially everted proboscis.

The peristomial segment is slightly emarginated laterally but less distinct on the dorsal and ventral surfaces. It is similar in length to the first setiger; tentacular cirri are absent (Fig. 1).

A relatively large, cylindrical, muscular proboscis is present and terminates anteriorly with four small papillae (Fig. 4). The opening of the proboscis is horizontal.

The first 6 setigerous segments are inflated and the surface epithelium may be weakly areolated delimiting a distinct anterior region. The parapodia in this region are reduced but increase in size up



Figures 1-3. *Parandalia ocularis*, new species. Figure 1. Anterior end in dorsal view x50. Figure 2. Parapodium 14 from left side in anterior view x100. Figure 3. Posterior end in ventral view x50.

to the sixth, which is similar in size to the succeeding parapodia. The first podium of the first setigerous segment lie in notopodial positions but a gradual shift to the neuropodial positions is completed by setiger 3 or 4.

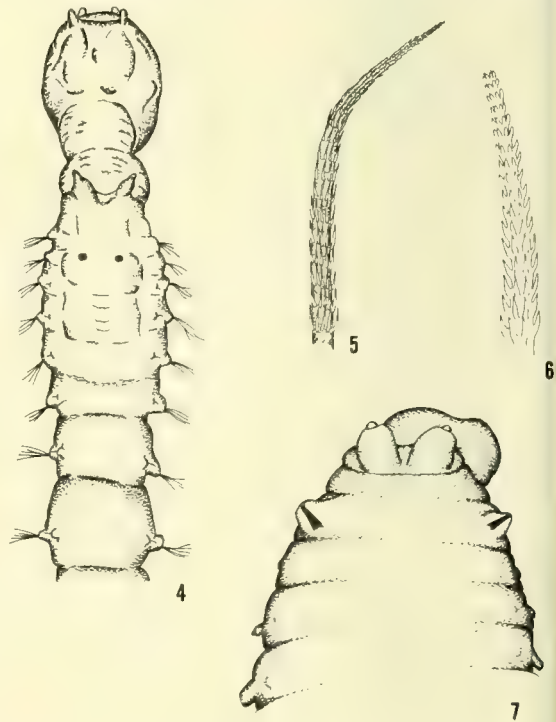
The first 2 setigerous segments have uniramous parapodia, all subsequent parapodia are unequally biramous. The first 3 notopodia on setigers 3-5 are reduced relative to those in subsequent segments, each notopodium bears 1 or 2 small, simple seta. The notopodia have become fully developed by setiger 9 or 10. A crystal-clear notopodial aciculum begins to protrude at setiger 9 becoming more fully exposed in succeeding segments.

When fully developed, each neuropodium is slightly tapering with a blunt, evenly rounded tip in all segments. The anteriormost neuropodia are reduced and do not become fully developed until setiger 6 or 7 (Fig. 1). The neuro-aciculum is fully embedded in most segments but may protrude slightly from the neuropodial lobe. A small papillar ventral cirrus at the outer basal edge of the neuropodium begins to appear about setiger 8. The cirrus is somewhat larger posterior to setiger 10 but retains the same shape in all setigers from the tenth setiger on. (Fig. 2).

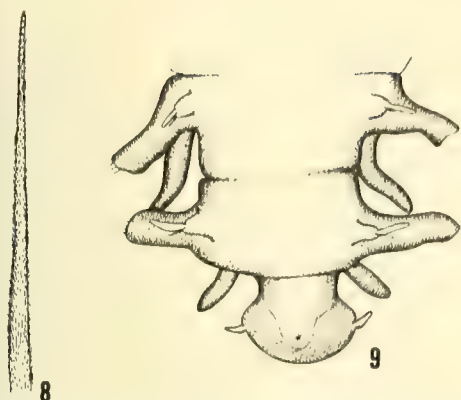
The first two neuropodial lobes each bear 4 geniculate, pointed, simple setae. The subsequent neuropodial setae are larger and may increase in number up to about 7. All neurosetae are born in a similar pattern (Fig. 2). Each neurosetae has a cylindrical stalk with an upper blade provided with many transverse rows of slender teeth (Fig. 5). The notopodial setae are short and nearly smooth.

The posterior end of the body tapers evenly and terminates in a rounded anal plaque (Fig. 3). Its margin is entire except for 3 anal cirrilike processes. Two cirri processes are lateral and one process is located mid-ventrally. The anal aperture is near the mid-ventral process and may be distinguished by a slight depression.

Discussion: Five species are known in the new genus *Parandalia*. Three specimens of *P. ocularis*, new species, were collected from the Santa Barbara Channel off southern California in silty-clay at depths of 23-25 fms. *P. fauveli*, Berkeley (1941) is known from the single type locality record in a mud flat near Newport Bay, California and generally from similar localities in southern California (Hartman, 1968). *P. americana* Hartman (1947) has been collected from sand flats at low tide near Biloxi, Mississippi and from the Gulf of Mexico



Figures 4-7. Anterior end in dorsal view x50 (4, 6) and distal end of neuroseta x950 (5, 7). Figure 4 and 5. *Parandalia ocularis*, new species, proboscis everted (4). Figure 6 and 7. *Loandalia aberrans*, Monro.



Figures 8, 9. *Loandalia aberrans*, Monro. Figure 8. Distal end of notoseta $\times 950$. Figure 9. Posterior end in dorsal view $\times 50$.

near San José Light, Guatemala in 12-13 fms. *P. indica* Thomas (1963) is known from the West Coast of India from muddy substratum in 7-10 fms. *P. gracilis* Hartman-Schröder (1959) has been collected off El Salvador.

P. ocularis is the only species having eyes; it is similar to *P. americana* and *P. fauveli* in that each has uniramous parapodia in the first segment and biramous parapodia continuous from the segment 2 or 3. *P. americana* and *P. fauveli* have emergent notopodial spines from the second and seventh setiger, respectively. These two species along with *P. gracilis* have been considered by Pettibone (1966) as synonymous with *P. fauveli*, although only the holotype of *P. fauveli* and two paratypes of *P. americana* were examined. *P. indica* is considered by the same author to be a doubtful species.

P. indica and *P. gracilis* are closely related species having biramous parapodia from the first segment. *P. gracilis* has 1 notopodial seta and *P. indica* has 2 notopodial setae on each segment.

Genus *Loandalia* Monro, 1936
Loandalia aberrans Monro, 1936

Loandalia aberrans Monro, 1936.

Material examined: DISCOVERY 274, off St. Paul de Loanda, Angola. From $8^{\circ}40'15''$ S, $13^{\circ}13'45''$ E to $8^{\circ}38'15''$ S, $13^{\circ}13'00''$ E, 64-65 m, grey mud, trawl, one specimen, holotype British Museum Natural History type number 1936-2-8-3376.

Remarks: A re-examination of the type species of the genus *Loandalia* showed that there are some details previously not reported by Monro (1936).

The anterior part of the body including the first 6 setigers is slightly inflated and the surface has a slight areolation; the median and posterior parts of the body are cylindrical. The posterior end was in

regeneration when the specimen was collected. The specimen is dull yellow with dark brown bars on each side of the notopodia in median and posterior setigers.

The prostomium is short and wide; prostomial palps are large compared to the size of the prostomium. A single peristomial segment is present; peristomial appendages are absent (Fig. 7). The proboscis was dissected out by Monro and could not be described from the remnants present.

The first 2 pairs of neuropodia are stout and conical; the first is dorsolateral in position; the second is in the normal position, somewhat ventral to the midline and directed ventrolaterally. All neuropodia from setiger 3 are similar; each has a long base with nearly parallel sides and a truncate distal margin; a small, button-shaped ventral cirrus is present near the inferior margin. The first indication of notopodial structures is on setiger 3; the notopodia are fully developed from setiger 9 and all notopodia are similar in median and posterior setigers. Each is conical and has a digitate dorsal cirrus. Each notopodial seta is slender and is evenly dense with fine hairs.

Branchiae are present from setiger 33 in all posterior segments except for the pygidium (Fig. 9). The first 10-15 pairs are short; all others are long, cirriform and project from the inner posteroventral margin of the neuropodia.

The pygidium is a small circular disk; 2 short lateral anal cirri and a single, mid-ventral anal cirrus present. The anus is on a ridge near the middle of the pygidium. As noted above, the posterior end of the specimen is in regeneration; the pygidium is thus probably considerably smaller than normal for this species (Fig. 9).

Each of the two first pairs of neuropodia has a single, thick, black aciculus with a rounded, blunt tip; setae are absent in these neuropodia. All other neuropodia have 2 closely similar kind of simple setae; near the superior margin is found 1 or 2 setae with a very coarse denticulation. The middle and inferior portion of the neuropodial fascicles consist of setae with fine denticles in closely packed whirls (Fig. 6). The neuropodial acicula are less than half as thick as the acicula in the two first neuropodia; each is yellow and bluntly cone-shaped. Acicula are absent in the notopodia; each has 2 to 3 short, slender setae. Each of the notopodial setae is cylindrical and finely pilose. Furcate setae were not observed.

The re-description of the type-specimen of *L. aberrans* differs from the original description in the following features. The exact distribution of branchiae were not mentioned by Monro and may be of some importance in separating this from

related species. Dorsal cirri or at least remnants of dorsal cirri, were found to be present on all notopodia. Such cirri were said to be absent in the original description. Monro reported the presence of thick, broken spines in the notopodia; no trace of any notopodial spines or notopodial acicula could be found in the re-examination; it is here suggested that Monro mistook the dorsal cirri for the notopodial spines usually present in the pilargiids.

Two thick, black acicula are present in each of the first neuropodia; these were mentioned by Monro, but he also assigned setae to the first neuropodia (Monro, 1936); no setae other than the acicula and no remnants of setae in the parapodial base were observed in the re-examination of the type.

The prostomium, and the peristomial segment are clearly separated from each other and from the first setiger.

The structure of prostomium and relationship between the different parts of the parapodia in *L. aberrans* are similar to those in other pilargiids. The genus *Loandalia* differs clearly from all other pilargiids in the presence of large, thick acicula in the anterior neuropodia and in the absence of notopodial spines and acicula. The presence of dorsal cirri in all notopodia separates it clearly from other species usually assigned to *Loandalia*; also branchiae have not been reported from any other member of this genus.

Distribution: The holotype and only known specimen of *L. aberrans* comes from Angola, West Africa in shelf depths.

ACKNOWLEDGMENTS

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TAXONOMY AND DISTRIBUTION OF THE ARCTIC SPECIES OF
LUCICUTIA (COPEPODA: CALANOIDA)

JULIO VIDAL¹

ABSTRACT: The taxonomy and distribution of the Arctic species of *Lucicutia* were studied. Analysis of approximately 400 plankton hauls from the Arctic Ocean revealed the presence of *Lucicutia polaris* Brodsky, *L. pseudopolaris* Heptner, and *L. anomala* Brodsky in samples collected in deep waters. The two former species are closely related but differ in morphological and biological characteristics of the adults and juvenile stages. The male of *Lucicutia anomala* is described for the first time. These species have a wide geographical distribution in the Arctic Ocean. They inhabit the Arctic bottom water and show different but overlapping ranges of vertical distribution. *L. pseudopolaris* is most abundant at a depth of about 1500 m; *L. polaris* preferentially lives at a depth of about 2000 m; and *L. anomala* is found in waters deeper than 2000 m. This species is most abundant at depths exceeding 3000 m. Physical, chemical and biological factors which might restrict the distribution of these species at different depths were discussed.

The plankton analyzed in this study is part of the collections of the Arctic project of the University of Southern California. The samples were collected from the drifting stations Arlis II and T-3 in the western Arctic Ocean, during the years 1952-1955 and 1964-1968, respectively. Horizontal tows at different depths of water and vertical tows in increments from bottom to surface were made with 0.5 m diameter closing nets of 62, 73, and 215 m mesh apertures and open nets of 73 and 215 m mesh apertures.

The male of *L. polaris*, and the adults and copepodite stages IV and V of *L. pseudopolaris* are described. Since *L. polaris* and *L. pseudopolaris* are closely related species, and since they are well represented in the Arctic Ocean, a detailed comparison of the external morphology of the adults and juvenile stages of these species was made.

The study on the vertical distribution of the species was based on the analysis of closing net samples. For this purpose horizontal tows at depths of 100, 500, 1000, 1500, 2000 and 3000m, and vertical tows at depths between 100-500m, 500-1000m, 1000-1500m, 1500-2000m, 2000-3000m, and below 3000m were considered. Since the vertical and horizontal tows were not quantitatively comparable, and the number of samples taken at different depths varied, the numerical values obtained in the analysis of vertical distribution of the species have been expressed in terms of percentages of relative abundance.

A list of stations at which plankton samples containing specimens of *Lucicutia* were collected has been deposited at the National Oceanographic Data Center. Reference specimens of the three species have been deposited in the collections of the Allan Hancock Foundation.

DESCRIPTION OF THE SPECIES

Lucicutia pseudopolaris Heptner, 1969
Figures 2a-m, 4e-m.

Lucicutia pseudopolaris Heptner, 1969.

Lucicutia polaris Brodsky, 1950 (♂ only); Hülse-
mann, 1966 (♂ only).

Measurements. Table 1.

Diagnosis. Total length 3.8 to 4.7 mm in the female and 3.6 to 4.4 mm in the male. Outline of the prosome ovate; anterior margin of the prosome rounded in dorsal and lateral view. Furcal rami as long as the abdomen. Antennules 24-segmented; in the female they exceed body length by the last 2-3 segments; in the male they reach the end of the furca. First pair of legs with 2-segmented endopodites; outer spine on the 1st exopodal segment reaches the distal third of the outer spine on

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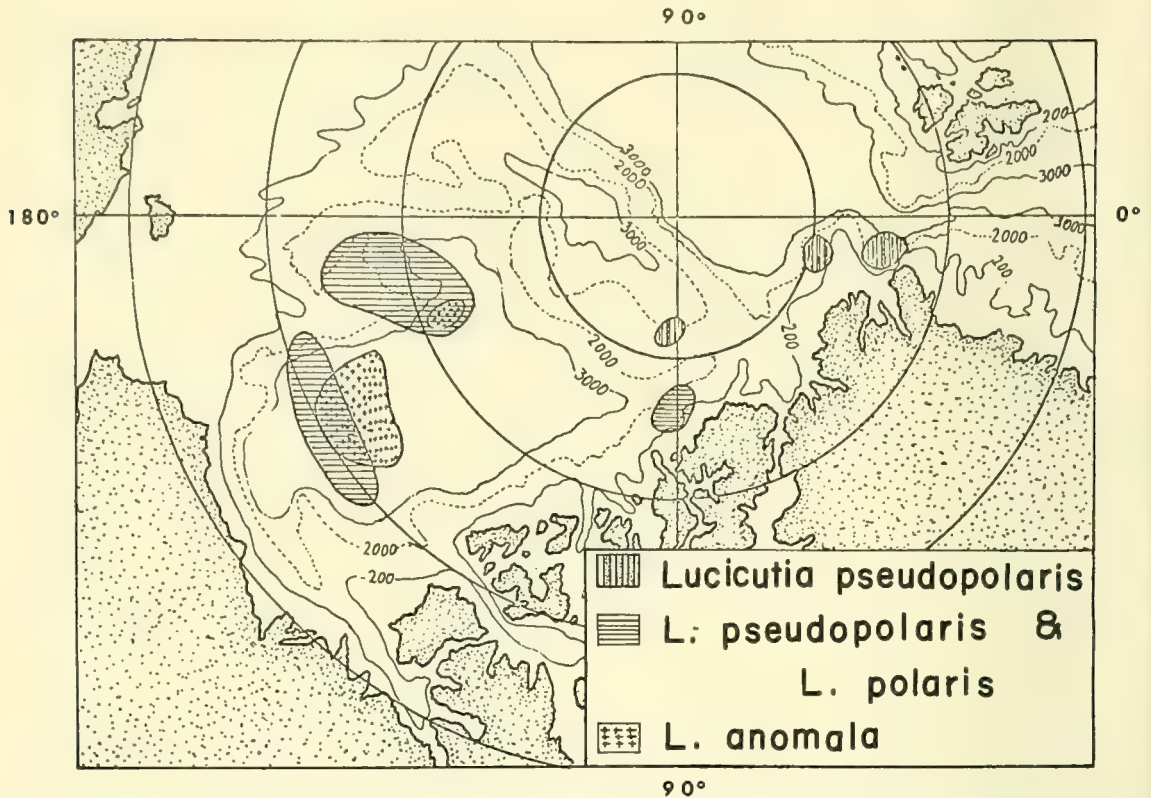


Figure 1. Occurrence of arctic species of *Lucicutia* in samples analyzed in this study.

exopodal segment 2. Female inner seta on exopodal segment 2 reaches beyond the base of inner seta 2 on exopodal segment 2.

Description. Adult female. The general shape of the body is robust. The outline of the prosome is ovate. The anterior margin of the cephalosome is rounded in dorsal and lateral view (Figs. 2a, b).

The urosome is 1.8-1.9 times as long as the prosome. The abdomen is nearly as long as the furcal rami. The genital segment is symmetrical in dorsal view (Fig. 2e); the genital protuberance is well developed and located in the proximal half of the segment (Fig. 2d). The furcal rami are long and thin, about 11 to 15 times longer than wide.

The antennules, 24-segmented, extend beyond the furca by the last 2-3 segments. Segments 1 and 2 fused.

The mandibular palp has 4 setae on the basal segment. The exopodite is 5-segmented, the endopodite 2-segmented; it is furnished with 4 setae on the proximal segment and 8 setae on the distal segment. The gnathobase of the mandible bears 9 or 10 teeth and a seta; the 4 proximal teeth are larger than the others.

The maxillule has 14 spines on the 1st inner lobe; 3 setae each on inner lobe 2 and 3; 3 setae on the basipodal segment 2; 9 setae on the endopodite; 11

setae on the exopodite and 5 setae on outer lobe 1.

The first pair of legs (Fig. 2f) has 3-segmented exopodites and 2-segmented endopodites. The outer spine on exopodal segment 1 reaches the distal third of the outer spine on exopodal segment 2.

Exopodites and endopodites have 3 segments on legs 2 to 4 (Fig. 2g). The outer distal margin of exopodal segments 1 and 2 of legs 2 and 3 are strongly projected.

The fifth pair of legs (Fig. 2h) has 3-segmented exopodites and endopodites. The inner seta on exopodal segment 2 reaches beyond the base of inner seta 2 on exopodal segment 3. Exopodal segment 3 is as long as the combined length of exopodal segments 1 and 2. The terminal spine on the exopodite is slightly shorter than the length of exopodal segment 3.

Adult male. Body shape (Figs. 2j, k) is as the female. The furcal rami are about 10 to 14 times as long as wide. The left antennule modified to serve as a weak clasping organ; the segments 1-2, 19-21, and 22-23 are fused. The right antennule reaches the end of the furca.

The appendages of the cephalosome and legs 1 to 4 of the metasome are as those of the female.

The basipodal segment 1 of the right 5th leg (Fig. 21) is longer than the corresponding segment

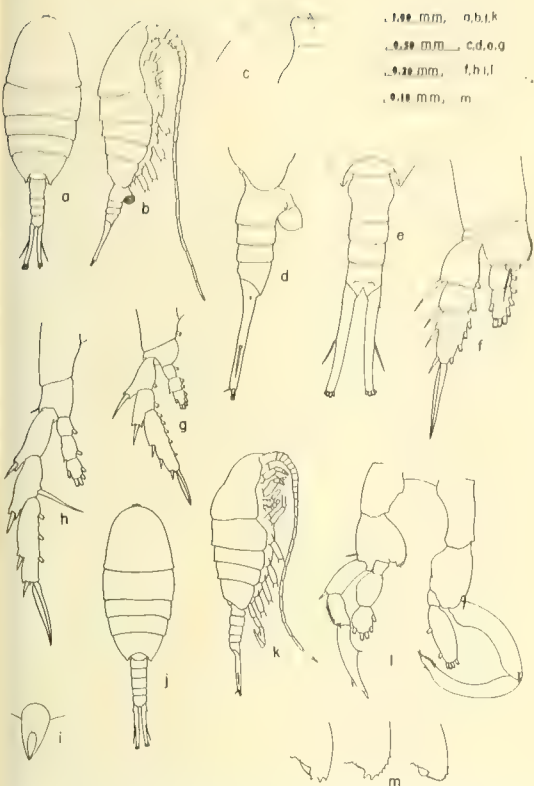


Figure 2. *Lucicutia pseudopolaris* Heptner. Female: a, dorsal view; b, lateral view; c, anterior part of cephalosome, lateral view; d, posterior part of body, lateral view; e, posterior part of body, dorsal view; f, first leg; g, second leg; h, fifth leg; i, rostrum. Male: j, dorsal view; k, lateral view; l, fifth leg; m, inner margin of second basal segment of right fifth leg in three different specimens.

of the left leg. Basipodal segment 2 of the left leg has a protrusion on its inner distal corner. This protrusion carries a row of teeth, variable in number and size (3-13), and a small rounded protuberance (Fig. 2m). The right side of the fifth pair of legs has a 2-segmented endopodite and exopodite. Exopodal segment 2 has 2 apical spines and 1 outer subapical spine. The left side of the fifth pair of legs has a 3-segmented exopodite and endopodite. Exopodal segment 3 has 1 outer, apical, and inner spine.

Copepodite Stage V. Body shape (Figs. 4j, 1) is as the adult. The cephalosome and metasomal segment 1 are separated; metasomal segments 4 and 5 are fused. The urosome is composed of 4 abdominal segments and the furca.

The antennules, 25-segmented, exceed the length of the body by the last 2-3 segments.

The first pair of legs has 3-segmented exopodites and 2-segmented endopodites (Fig. 4j). Legs 2 to 4 have 3-segmented exopodites and endopodites.

The fifth pair of legs has 2-segmented endopodites and exopodites in both sexes (Figs. 4k, m). The distal segment corresponds to fused segments 2 and 3. In the male the right side of leg 5 is shorter than the left.

Copepodite Stage IV. The specimens of this stage have a 3-segmented abdomen (Figs. 4e, f). Exopodites and endopodites of legs 1-4 have 3 segments (Fig. 4g). The fifth pair of legs has 1-segmented endopodites and exopodites.

Distribution. *L. pseudopolaris* has a wide geographical distribution in the Arctic Ocean. It has been recorded by Heptner (1969) from an area between 76°38' N and 81°12' N and 173°44' E and 189°35' E, and at 88°10' N 82°22' W. In our collections it was found between 72°42' N and 83°27' N and 9°15' W and 157°12' W.



Figure 3. *Lucicutia polaris* Brodsky. Female: a, dorsal view; b, lateral view; c, anterior part of cephalosome, lateral view; d, posterior part of body, lateral view; e, posterior part of body, dorsal view; f, first leg; g, second leg; h, fifth leg. Male: i, dorsal view; j, lateral view; k, fifth leg; l, inner margin of second basal segment of right fifth leg in two different specimens. Stage V copepodite, female: m, dorsal view; n, lateral view; o, first leg; p, fifth leg. Stage V copepodite, male: q, dorsal view; r, fifth leg.

Lucicutia polaris Brodsky, 1950

Figures 3a-r, 4a-d.

Lucicutia polaris Brodsky, 1950 (♀ only); Johnson, 1963; Heptner, 1969.

Not *Lucicutia polaris* Brodsky, 1950; Hülsemann, 1966; Grice and Hülsemann, 1967.

Measurements. Table 1.

The female of *Lucicutia polaris* was described by Brodsky (1950). Heptner (1969) transferred the male described by Brodsky under this name to a new species, *L. pseudopolaris*. In the same place Heptner described the male of *L. polaris* for the first time.

L. polaris is similar to *L. pseudopolaris*, however, both are separate species with the following morphological differences: *Adult female*: *Lucicutia polaris* differs from *L. pseudopolaris* in the shape of the cephalosome. In dorsal view, the anterolateral margin of the cephalosome of *L. polaris* has slight lateral projections (Fig. 3a) which is not present in the cephalosome of *L. pseudopolaris* (Fig. 2a). In lateral view, the anterior margin of the cephalosome of *L. polaris* is depressed (Figs. 3b, c), whereas that of *L. pseudopolaris* is rounded (Figs. 2b, c).

The length ratios of the prosome-urosome and abdomen-furca are smaller in *L. polaris* than in *L. pseudopolaris* (Table 1).

The appendages of the cephalosome are not significantly different in both species. The external spines on the exopodal segments of the first 4 pairs of legs are slightly shorter in *L. polaris* (Figs. 3f-h) than in *L. pseudopolaris* (Figs. 2f-h).

On the fifth pair of legs of *L. polaris* the inner seta on exopodal segment 2 does not reach the base of inner seta 2 of the exopodal segment 3 (Fig. 3p); whereas, in *L. pseudopolaris* it extends beyond the base of inner seta 2 of exopodal segment 3. Exopodal segment of *L. polaris* is longer than exopodal segments 1 and 2 together; whereas, in *L. pseudopolaris* it is as long as the combined length of these segments.

Adult male. In general, the morphological differences found in the female are also present in the male. The fifth pair of legs differs from that of *L. pseudopolaris* by the presence of 3 to 6 teeth on the inner margin of the left basipodal segment 2, and by the presence of an additional spine on the middle part of the distal segment of the right exopodite (Fig. 3k).

Copepodite Stages V and IV. The overall appearance of the body is as that of the adults. The differences between the juvenile stages of *L. polaris* and of *L. pseudopolaris* are similar to those found in the adult of both species. They differ mainly by the shape of their cephalosome, as described for

the adults. In *L. polaris*, the total length of the body, and the length ratios of the prosome-urosome and abdomen-furca are smaller than those in the juvenile stages of *L. pseudopolaris* (Table 1).

Distribution. *L. polaris* has been recorded from the central part of the Arctic Ocean (Brodsky, 1950; Johnson, 1963; Heptner, 1969) and from the north Pacific Ocean (Heptner, 1969). In our collections it was found in the area between 75°03' N and 83°15' N, and 90°30' W and 173°36' W. *L. polaris* has also been reported from the Indian Ocean and southeastern Pacific Ocean (Hülsemann, 1966; Grice and Hülsemann, 1967). These records probably correspond to species from the southern Pacific and Indian Ocean rather than to the species *L. polaris* described by Brodsky from the Arctic Ocean.

Lucicutia anomala Brodsky, 1950

Figures 4n-s.

Lucicutia anomala Brodsky, 1950; Grice and Hülsemann, 1965; Hülsemann, 1966.

Measurements. Table 1.

Brodsky (1950) described the female of *L. anomala*. The male is here described for the first time.

Adult male. The general shape of the body (Figs. 4n, o) and of the appendages agree very closely with those described for the female (Brodsky, 1950).

The left antennule is modified to serve as a weak clasping organ. The segments 1-2, 19-21, and 22-23 are fused. The right antennule reaches the end of the furca.

The 1st pair of legs has 3-segmented endopodites (Fig. 4q).

The right side of the fifth pair of legs (Fig. 4r) has a 2-segmented exopodite and endopodite; basal segment 1 is slightly longer than the corresponding segment on the left leg; basipodal segment 2 of the right side has a smooth projection on the outer distal margin; exopodal segment 2 has 2 apical spines. The left leg has a 3-segmented exopodite; the inner projection of basipodal segment 2 has a row of 5 to 11 small teeth (Fig. 4s); exopodal segment 3 bears 1 apical and 1 inner spine.

Distribution. This species has been recorded from the Arctic Ocean (Brodsky, 1950) and northeastern Atlantic Ocean (Grice and Hülsemann, 1965). In our collections it was found in the area between 75°18' N and 77°51' N, and 140°40' W and 157°12' W.

EPIZOIC SUCTORIANS

Epizoic suctorians were observed on these three species of *Lucicutia*. The number of species of suctorians is uncertain. The rates of incidence on

TABLE I. Measurements and length ratios of the Arctic species of *Lucicutia*

	TOTAL LENGTH (MM)*				PROSOME-UROSOME LENGTH RATIO			ABDOMEN-FURCA LENGTH RATIO		
	N	Mean	Range	St. Dev.	Mean	Range	St. Dev.	N	Mean	Range
<i>Lucicutia pseudopolaris</i>										
Adult female	37	4.27	3.81-4.75	0.206	1.87: 1	1.70-2.15	0.096	20	0.97: 1	0.82-1.06
Adult male	20	4.07	3.68-4.43	0.177	1.73: 1	1.56-2.00	0.114	18	0.98: 1	0.88-1.10
Copepodite Stage V female	9	3.27	3.10-3.56	0.148	2.11: 1	1.90-2.27	0.127	9	1.04: 1	0.91-1.20
Copepodite Stage V male	7	3.27	3.13-3.41	0.089	2.07: 1	1.86-2.31	0.135	7	1.05: 1	0.94-1.18
Copepodite Stage IV	5	2.55	2.46-2.64	0.064	2.32: 1	2.26-2.41	0.055	5	1.08: 1	1.04-1.11
<i>Lucicutia polaris</i>										
Adult female	29	3.76	3.50-4.06	0.132	1.68: 1	1.48-1.90	0.097	20	0.82: 1	0.67-1.00
Adult male	24	3.68	3.25-4.06	0.197	1.60: 1	1.46-1.72	0.079	20	0.83: 1	0.72-0.96
Copepodite Stage V female	12	2.84	2.76-2.98	0.060	1.87: 1	1.75-2.00	0.085	12	0.89: 1	0.77-0.94
Copepodite Stage V male	2	2.87	2.76-2.98	—	1.91: 1	1.90-1.93	—	2	0.89: 1	0.87-0.91
Copepodite Stage IV	4	2.10	2.06-2.18	0.045	2.26: 1	2.09-2.40	0.112	4	0.85: 1	0.81-1.04
<i>Lucicutia anomala</i>										
Adult female	9	2.50	2.43-2.58	0.043	1.75: 1	1.62-1.85	0.058	9	0.74: 1	0.66-1.06
Adult male	7	2.42	2.30-2.50	0.080	1.71: 1	1.66-1.77	0.044	7	0.78: 1	0.75-0.83
Copepodite Stage V	2	2.01	2.00-2.03	—	1.97: 1	1.86-2.09	—	2	0.82: 1	0.79-0.86

*N= number of specimens; St. Dev. = sample standard deviation

their hosts varied on the three species of *Lucicutia* (Table 2).

L. polaris carried at least 4 or 5 different species of suctorians and had the highest rate of incidence.

L. pseudopolaris seemed to have 3 different species of epizoa and a lower rate of incidence.

L. anomala carried only 1 species of suctorians and had the lowest rate of incidence.

Suctorians were observed on adults and juvenile stages. In general, the rate of incidence was slightly

higher in males than in females. The areas of the body with a higher number of epizoa were the furca and anal segment and, in the male, also the basipodal segments of the fifth pair of legs. Low rates of incidence were observed on other surfaces of the body and on metasomal appendages.

VERTICAL DISTRIBUTION OF THE SPECIES

The three species of *Lucicutia* discussed in this paper are widely distributed in the Arctic Ocean.

TABLE II. Rate (%) of incidence of suctorians on the species of *Lucicutia*

	<i>L. polaris</i>	<i>L. pseudopolaris</i>	<i>L. anomala</i>
Female	65	11	12
Male	77	29	12
Stage V	42	32	—

They inhabit deep water, the Arctic Bottom Water, and show different but overlapping ranges of vertical distribution.

L. pseudopolaris is abundant at a depth of about 1500 m and diminishes gradually in abundance from there to disappear above 1000 m and below 3000 m. *L. polaris* seems to inhabit depths between 1500 m and less than 3000 m. It was found in greatest numbers at a depth of about 2000 m. *L. anomala* lives in deeper water from about 2000 m to more than 3000 m. It is more abundant at depths exceeding 3000 m (Fig. 5).

The Arctic bottom water, as defined by Coachman (1963), is a homogeneous water mass below about 900 m depth, with average temperatures from 0.0 to -1.0°C and salinities from 34.90 ‰ to 34.99 ‰. Other studies and oceanographic data have demonstrated that chemical parameters such as oxygen, phosphate and silicate have a remarkable uniformity in this water mass (Kusunoki *et al.*, 1966; Muguruma, 1961; English, 1961). Among the physical parameters, light is not likely to be a controlling factor for the vertical distribution of Arctic species at the depths in question. Consequently, it seems that among the measured physico-chemical parameters the only one which might have a major effect on the vertical distribution of these species could be pressure.

Among the biological factors which might restrict these species to different ranges of depths we must consider food availability and competition for food. English (1963) briefly discussed the possible sources of food for zooplankton in the Arctic Ocean, and suggested that the production of particulate food by secondary producers of the nanoplankton could play a more important role in the Arctic Ocean than in other areas. In regard to the Arctic bottom water, it is likely that food for filter-feeders can be provided by the local secondary producers of the nanoplankton, and by sinking of dead organisms, detritus, and aggregates of organic matter from the upper layers. Several studies on the formation, distribution, and role of detritus and aggregates of

organic matter in the sea (Parsons and Strickland, 1962; Riley, 1963; Menzel and Goering, 1966; Jørgensen, 1966; Johannes, 1967) concluded that they can be considered as a very important potential source of food for filter feeders.

A close relationship between the feeding habits of calanoid copepods and the structure of their oral appendages was experimentally shown by Anraku and Omori (1963). The comparison between the oral appendages of the Arctic species of *Lucicutia*, and those studied by Anraku and Omori, indicated that *Lucicutia* has characteristics of herbivorous and omnivorous forms. The mesh formed by the setules of the maxillae, the filtering appendages, is of about 5 to 10 μ in *L. pseudopolaris* and *L. polaris* and slightly smaller than 5 μ in *L. anomala*. This fine mesh and the structure of the oral appendages

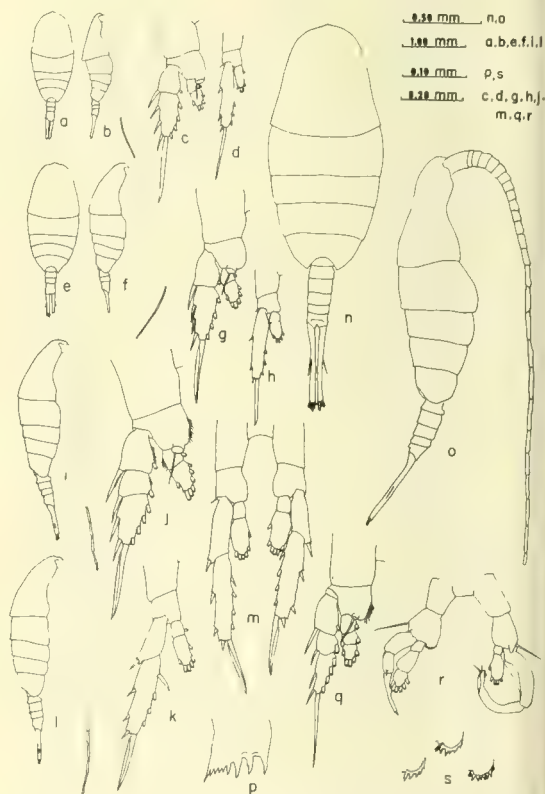


Figure 4 — *Lucicutia polaris* Brodsky. Stage IV copepodite: a, dorsal view; b, lateral view; c, first leg; d, fifth leg. *Lucicutia pseudopolaris* Heptner. Stage IV copepodite: e, dorsal view; f, lateral view; g, first leg; h, fifth leg. Stage V copepodite, female: i, lateral view; j, first leg; k, fifth leg. Stage V copepodite, male: l, lateral view; m, fifth leg. *Lucicutia anomala* Brodsky. Male: n, dorsal view; o, lateral view; p, mandibular gnathopod; q, first leg; r, fifth leg; s, inner margin of second basal segment of right fifth leg in three different specimens.

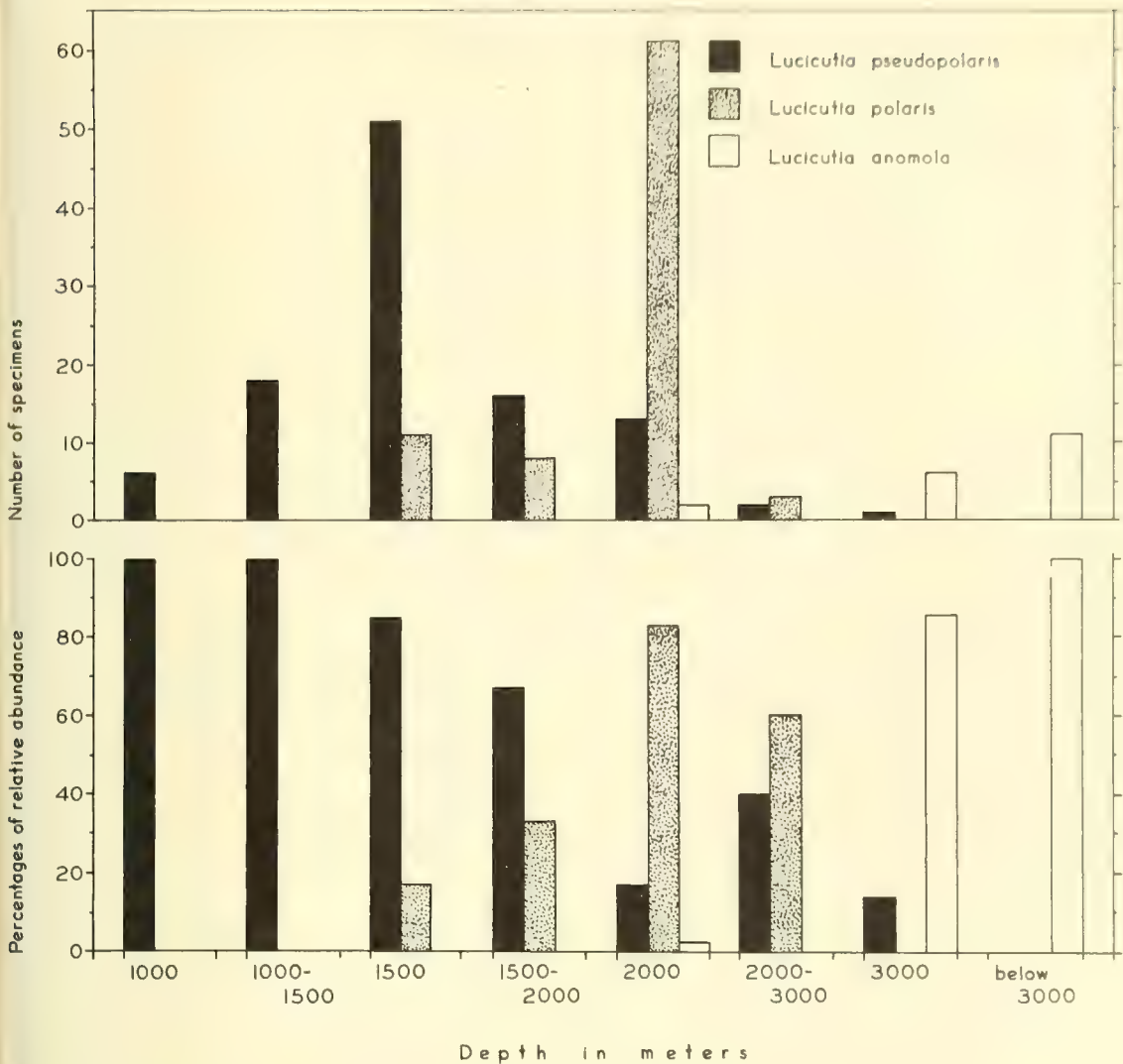


Figure 5 — Percentages of relative abundance and number of specimens of the arctic species of *Lucicutia* at different depths.

intermediate between herbivorous and omnivorous forms, would permit these species to feed on aggregates of organic matter and detritus, which range in size from about 1 μ to several mm, and on small organisms of the nannoplankton. The absence of morphological differences in the structure of the oral appendages (especially between *L. pseudopolaris* and *L. polaris*) suggests that the above species are feeding on the same or on a very similar food supply.

Related species can avoid or reduce competition for food by distributing themselves at different depths. Marshall (1954; 1963) discussed the vertical distribution of related species of fishes (*Vinciguerria* spp; *Cyclothone* spp; *Stomias* spp;) and gave examples of vertical exclusion. Other examples of sharp

stratification of related species of pelagic organisms were given by Banse (1964). In general, this behavior might permit a reduction of competition for food and a better utilization of the ecosystem.

It is likely that the vertical distribution and stratification of the Arctic species of *Lucicutia* are the outcome of the interactions of all environmental factors through time — physical factors such as pressure, chemical, and more likely biological factors — tending to a better utilization of the food niches with consequent reduction of interspecific competition and better possibilities of survival.

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A REVIEW OF THE GENUS *BOCCARDIA* CARAZZI (POLYCHAETA: SPIONIDAE) WITH DESCRIPTIONS OF TWO NEW SPECIES

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ABSTRACT: Taxonomic characteristics of 14 species of *Boccardia* are compiled in the form of a table. Each species is further distinguished in a key. *Boccardia ligerica* Ferronniere is redescribed with new synonymies. Two new species, *B. berkeleyorum* and *B. chilensis* are described.

The present paper is fourth in a series on *Boccardia* taxonomy. The first three (Woodwick, 1963a; 1963b; Blake, 1966) dealt with *B. tricuspa*, *B. columbiana*, *B. proboscidea* and *B. hamata*. Adults were described and observations on ecology recorded. In the present study two species new to science are described. *Boccardia berkeleyorum* comes from central California while *B. chilensis* comes from the coast of Chile. In addition, *B. ligerica*, a European species, is redescribed and new synonymies presented. Differential characteristics of known species of the genus are summarized in Table I. Analysis of the critical characteristics reveals that several well-defined groups of species are present. Discussion of these relationships follows the species descriptions.

Specimens of *Boccardia berkeleyorum* were collected by us during the years 1961-63. The *B. chilensis* material was included among the collections of the Lund University Chile Expedition 1948-49, the sedentary polychaetes of which are now at the Allan Hancock Foundation. We are grateful to Dr. Kristian Fauchald for the loan of this material. Specimens of *B. ligerica* were kindly sent by the Zoological Museum of Amsterdam (ZMA) and Dr. Francois Rullier of the Université de Catholique, Angers, France.

Information included in Table I comes mostly from published sources. We are grateful to Dr. Bernard McAlice of the University of Maine for his translation of the article by Khlebovitsch.

This study was supported in part by N.S.F. Grants G-17990) and (GB-1264). Additional studies on *Boccardia* larval development have been completed and will be published in a subsequent paper.

SYSTEMATICS

Genus *Boccardia* Carazzi, 1893

Type species: Boccardia polybranchia (Haswell) 1885.

Synonyms: ?Perialla Kinberg, 1866.

Diagnosis: Prostomium rounded or bifid anteriorly, extending posteriorly as a caruncle. Eyes present or absent. First setigerous segment with or without notosetae. Setiger 5 greatly enlarged, with heavy spines of either one or two types, arranged in a curved row. Posterior notosetae may include specialized spines, hooks and/or simple capillaries. Hooded hooks begin on setiger 7. Branchiae begin on segments anterior to setiger 5 and are not fused to the notopodial lobes. Pygidium enlarged or reduced, saucerlike or divided into lobes.

The following species of *Boccardia* are herein considered valid and are included in Table I. Synonymies are in parentheses; asterisk indicates a new synonymy.

1. *B. basilaria* Hartman, 1961
2. *B. berkeleyorum* new species
3. *B. chilensis* new species
4. *B. columbiana* Berkeley, 1927
5. *B. hamata* (Webster), 1879
(*B. uncata* Berkeley, 1927)
(*Polydora uncatiformis* Monro, 1938)
6. *B. ligerica* Ferronniere, 1898
(**Polydora redeki* Horst, 1920)
7. *B. natrix* (Söderström), 1920
8. *B. perata* (Khlebovitsch), 1959
9. *B. polybranchia* (Haswell), 1885
10. *B. proboscidea* Hartman, 1940
(?*Spio californica* Fewkes, 1889)
(?*Polydora californica* Treadwell, 1914 HOMONYM)
11. *B. pseudonatrix* Day, 1961
12. *B. tricuspa* (Hartman), 1939
13. *B. truncata* Hartman, 1936
14. *B. sp.*

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(*Polydora redeki* *sensu* Okuda, 1937, not Horst, 1920)

Boccardia ligerica Ferronniere Emended
Figure 1

Boccardia ligerica Ferronniere, 1898; Fauvel, 1927; ?Day, 1955, 1967.

Polydora redeki Horst, 1920; Fauvel, 1927; Augener, 1939; Hempel, 1957a, 1957b; Rullier, 1960.

Material examined: Holland, Zuider Zee under rock, October 11, 1932, ZMA 1156 (30 specimens); France, Benouville, April 25, 1953, coll. François Rullier, (6 specimens).

Description: Complete specimens from Holland measure up to 12 mm and have about 70 segments. The French material contains only anterior fragments.

The prostomium is weakly bifid on its anterior margin (Fig. 1a). The caruncle extends posteriorly to setiger 2 or 3. There is no nuchal tentacle. There are 4 eyes; a widely spaced anterior cup-shaped pair, and a posterior pair closely spaced and oval in shape (Fig. 1a).

Setiger 1 is reduced; it has small notopodial lobes, no notosetae, and only a small fascicle of capillary neurosetae (Fig. 1a). Setigers 2, 3, 4, -, 6 and succeeding setigers contain spreading fascicles of winged capillary notosetae. The number of these setae diminishes in posterior setigers where they are replaced by stout capillary setae and a specialized recurved hook (Fig. 1g). The parapodia in posterior segments are modified in a manner similar to those of the closely related *B. hamata* (Blake, 1966). They are laterally elevated leaving a dorso-median channel between them. The recurved notopodial hooks project medially towards this channel (Fig. 1i).

The neurosetae of setigers 2, 3, 4, -, and 6 contain fascicles of winged capillary setae. Bidentate hooded hooks which begin on setiger 7 largely replace the capillary setae. The hooks number 5 or 6 in a series with 1 or 2 ventral slender capillary setae. In posterior setigers the hooks number 2 or 3. The structure of the hooded hooks is similar to that of *B. hamata* (Blake, 1966). The 2 teeth have only a slight angle between them and there is no constriction on the shaft (Fig. 1h). Angle between the shaft and the main tooth is obtuse.

Setiger 5 is about twice as large as preceding and succeeding setigers. It is modified and contains a row of heavy spines (Fig. 1b) alternating with lanceolate companion setae (Fig. 1c-d). The heavy spines are simple, falcate and have no accessory structures. Dorsal to the row of heavy spines is a small group of stout geniculate setae (Fig. 1e) and

ventral to it is a small tuft of pointed geniculate setae (Fig. 1f).

Branchiae occur on setigers 2, 3, -, -, -, 7 and succeeding setigers for about one-third the length of the worm.

The pygidium consists of a flattened plate from which 2 anal cirri arise. The anus opens on the dorsal side (Fig. 1i).

Remarks: In the past *Polydora redeki* and *Boccardia ligerica* have been maintained as separate species as a result of the lack of complete specimens and confusion among investigators on the reported distribution of the branchiae. Most descriptions of the posterior segments have been incomplete.

Boccardia ligerica was described by Ferronniere (1898) from the Estuary of Loire, France. His general description and figures were adequate, but his observations on the branchiae were vague. His written description suggested that the anterior branchiae were distributed on setigers 2, 3, 4, -, -, 7 . . . , although his figures show anterior branchiae only on setigers 2 and 3. He adequately described the pygidium and clearly illustrated the two anal cirri, one of which appears to have been broken. Fauvel (1927) repeated Ferronniere's earlier description and Day (1955; 1967) in describing a South African specimen referred it with question to *B. ligerica*.

Polydora redeki was described from Holland by Horst (1920). His figures clearly show branchiae on setigers 2, 3, -, -, -, 7. Fauvel (1927) repeated Horst's description. Augener (1939) briefly described *P. redeki* from northern Germany. He figured the pygidium as a simple plate without processes. Friedrich (1938) did not add to the description. Hempel (1957b) did not describe the adult morphology in her paper on tube building. Rullier (1960) redescribed the species and for the first time elucidated the true structure of the pygidium. He reported the anterior branchiae as occurring on setigers 2, 3, 4, -, -, 7. The branchiae of setiger 5 were said to be smaller than on 2 and 3; however his figures do not show branchiae on setiger 4. His descriptions and illustrations of the post-larva stage of 14 setigers show the branchiae as being on setigers 2, 3, -, -, -, 7. Rullier's description and figure of the pygidium are like Ferronniere's figure for *B. ligerica*.

An examination of specimens from France collected and sent by Rullier and additional material from the Zuider Zee of Holland collected in 1932 proved that specimens from the two localities were the same. Only the material from Holland contain complete specimens. The anterior ends of the specimens from the two localities were identical. Branchiae were limited to setigers 2, 3, -, -, -, 7.

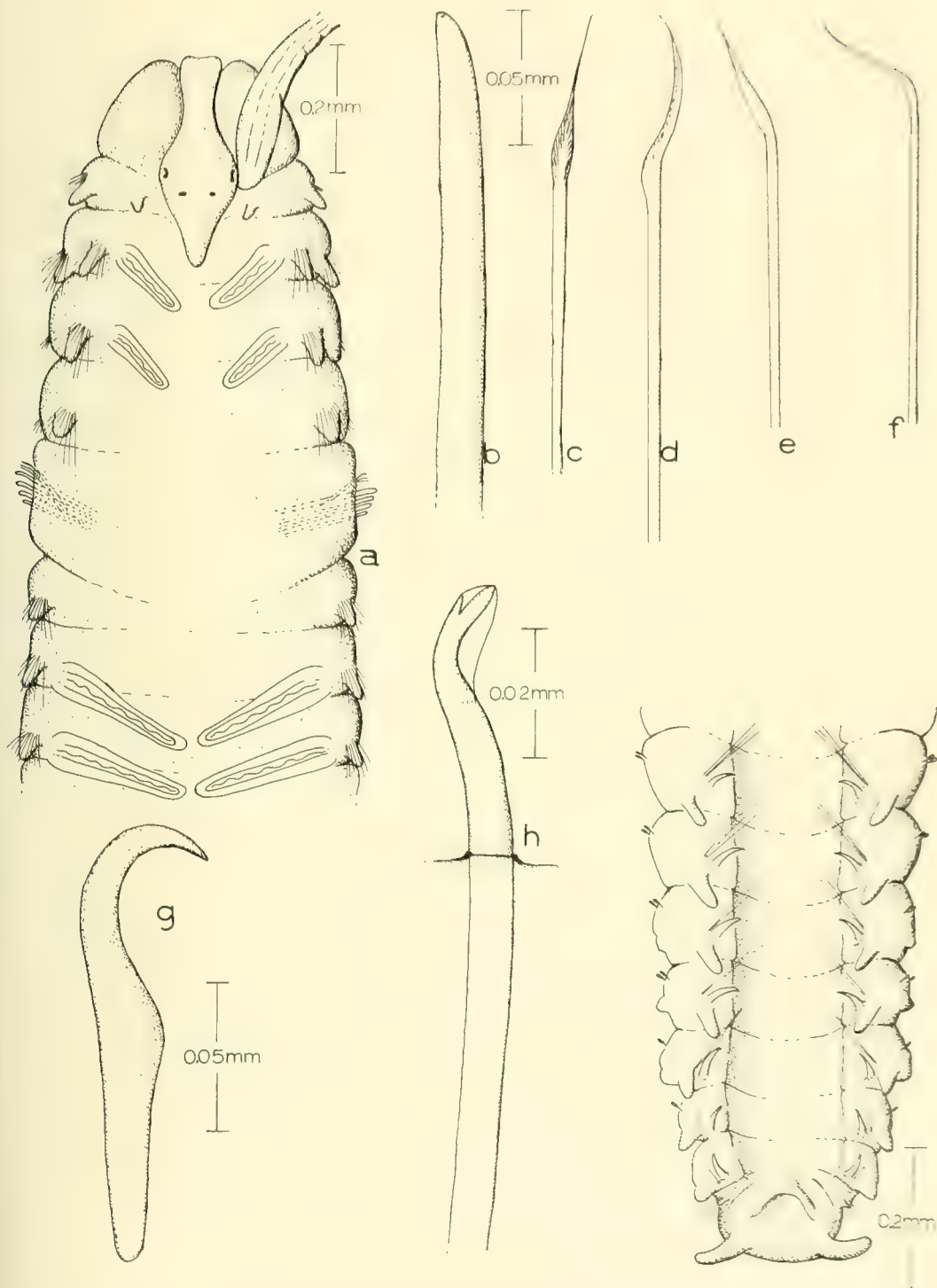


Figure 1. *Boccardia ligERICA* Ferronniere: a, anterior end in dorsal view; b, heavy spine from setiger 5; c-d, companion setae from setiger 5; e, dorsal setae from setiger 5; f, neurosetae from setiger 5; g, posterior notopodial spine; h, hooded hook from setiger 10; i, posterior end in dorsal view.

With the absence of branchiae on setiger 4 of all specimens examined and the lack of any figures which show branchiae on that setiger from the published descriptions of Horst (1920), Ferronniere (1898) and Rullier (1960) we conclude that *Boccardia ligerica* and *B. redeki* are synonymous. Since *ligerica* is the older name, it has priority over *redeki*.

Okuda (1937) and Imajima and Hartman (1964) have described a species of *Boccardia* from Japan which was identified as *B. redeki*. It is closely related to *ligerica*, *hamata* and *truncata* but one important difference is the presence of a nuchal tentacle (Table I).

Hartman (1941; 1961; 1969) referred some posteriorly incomplete California specimens to *B. redeki*. *Boccardia ligerica* is closely related to *B. hamata*. The two differ in the structure of the pygidium and the distribution of the branchiae (Table I). Because *B. hamata* is common in California waters, it is possible that the incomplete specimens described by Hartman are *B. hamata*. *Ecology and distribution*: *Boccardia ligerica* occurs in brackish waters of mud flats of western Europe including Holland, France and Germany; ?South Africa. Associated organisms include the amphipods *Corophium volutator* Pallas and *C. lacustre* Vanhoffen and the polychaetes *Mercierella enigmatica* Fauvel, *Neanthes diversicolor* (O. F. Müller) and *Neanthes succinea* (Frey and Leuckart) (Rullier, 1960).

***Boccardia berkeleyorum*, new species**

Figure 2

Material examined: California: Cayucos, August 28, 1961, hermit crab shells, (8, TYPE); March 3 (2), April 28 (5), July 3, 1962 (8) from coralline algae; Morro Bay, October 24, 1961, from shells of *Pododesmus machroschisma* (Deshayes) (1); May 18, 1963, from *Pododesmus* (5); San Simeon Beach State Park, December 19, 1961, from hermit crab shells (1); Fort Bragg, June 20, 1962, from coralline algae (1); Eureka (Trinidad Head), June 21, 1962, from hermit crab shells (1).

The holotype is deposited in the Allan Hancock Foundation, University of Southern California and was collected at Cayucos (San Luis Obispo County) from burrows in *Tegula brunnea* (Philippi) occupied by the hermit crab, *Pagurus granosimanus* (Stimpson). The collections were made on August 28, 1961 from rocks at mid-tide level. Additional specimens taken at this station have been designated as paratypes and deposited in the Allan Hancock Foundation and the United States National Museum, Washington, D.C. Additional collections remain with the authors.

It is a pleasure to name this species in honor of

Edith and Cyril Berkeley who have made significant contributions to the systematics of polychaetes.

Description: Specimens in the present collections measure 5-14 mm and have up to 100 setigerous segments. There is no noticeable body pigmentation.

The prostomium is rounded on its anterior margin (Fig. 2a). The prostomial ridge is elevated and enlarged at the level of setiger 1; it continues posteriorly as a stout caruncle to near the posterior border of setiger 3. Palps on preserved specimens extend posteriorly to about setiger 12, but are much longer on live forms. There are no eyes.

Setiger 1 lacks both notosetae and a notopodial lobe (Fig. 2a). There is a small fascicle of slender capillary neurosetae and a bluntly rounded lobe on the first setiger. Setigers 2, 3, 4, -, 6 and succeeding setigers have posteriorly directed winged capillary notosetae arranged in 2 bundles. The second bundle has longer setae. In the posterior one-third of the body the winged capillary setae are replaced by longer capillary setae and heavy acicular spines (Fig. 2 j-k). The heavy spines are simple in structure and do not have the hooked appearance as in *B. hamata* and *B. ligerica*. The neuropodia of setigers 2, 3, 4, -, and 6 have fascicles of winged capillary setae. Bidentate hooded hooks begin on setiger 7. There are 5 or 6 hooks at first, accompanied by a single capillary seta. The number of hooks does not exceed 7 per neuropodium and in posterior setigers is reduced to 3 or 4. The hooks have 2 teeth nearly equal in size separated by an angle of about 90° (Fig. 2 h-i).

Setiger 5 is larger than preceding and succeeding setigers and contains modified setae (Fig. 2a). The dorsal setae are modified and include two types of heavy spines. The first is simple and falcate (Fig. 2 f-g). The second is bushy-topped and has a small accessory tooth (Fig. 2 b-e). Ventral to the heavy spines is a small tuft of capillary setae.

Branchiae are flattened and fingerlike in outline (Fig. 2a). They are small on setiger 2, 3, 4, -, 6 and 7, while those on 8 and succeeding setigers are much larger. Branchiae are reduced in size near the mid-body and are absent from the posterior one-fourth of the body.

The pygidium is composed of 4 small individual lobes which surround the anal opening (Fig. 2k). Variability in size of the pygidial lobes in the present specimens may be an artifact of preservation.

Remarks: The similarity between the modified setae of *Boccardia berkeleyorum* and *Polydora anophthalma* Rioja (1962) is apparent. Type material for *P. anophthalma* is no longer in existence precluding verification of its branchial distribution. Rioja did not describe the pygidium and ascribed the branchiae as beginning on setiger 8. He stated

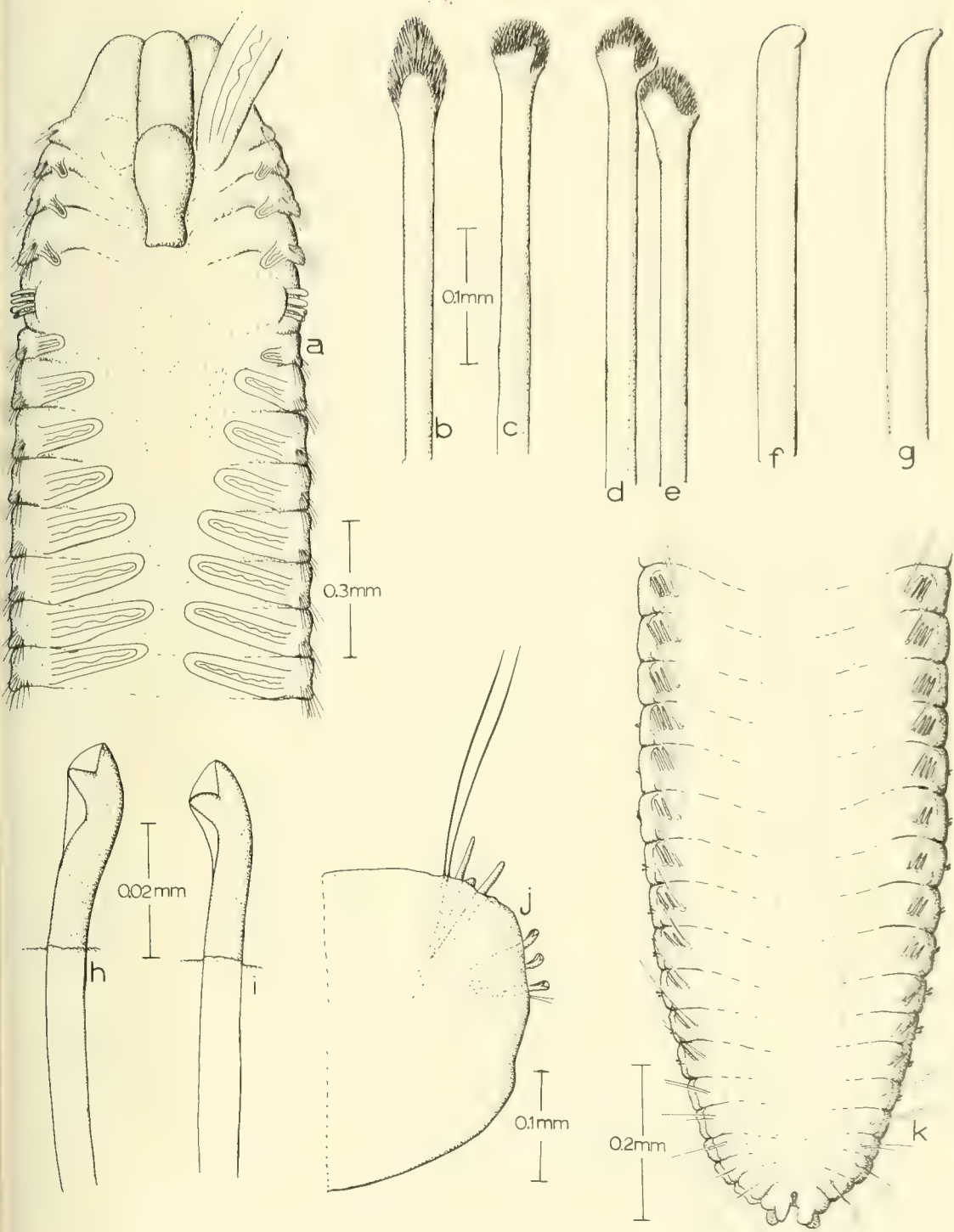


Figure 2. *Boccardia berkeleyorum* new species; a, anterior end in dorsal view; b-e, bristle-topped heavy spines from setiger 5; f-g, falcate spines from setiger 5; h-i, hooded hooks from setiger 12 seen at two angles; j, posterior setiger in posterior view; k, posterior end in dorsal view.

that posterior spines were absent. The bushy-topped setae which he described for the fifth setiger are very similar to those of *B. berkeleyorum*; however, the second type of setae are somewhat different. Rioja's figure 91 suggests a bifid nature. In *B. berkeleyorum* the second type has a simple falcate structure, but if viewed from a certain angle the beak of the spine may give a pseudo-bifid appearance.

Boccardia berkeleyorum is unique among species of the genus in the possession of special posterior spines which are acicular. In this respect it approaches certain species of the closely related genus *Polydora*. The species, *P. quadrilobata*, *P. caulleryi*, and *P. armata* each have awllike posterior spines but differ strikingly in the setation of the fifth setiger and lack of anterior branchiae, characteristic of species of the genus *Boccardia*.

The occurrence of different types of posterior spines throughout species of the polydorid complex may be the result of convergent evolution of species of various genera.

Ecology and distribution: *Boccardia berkeleyorum* was found in central California at Morro Bay, Cayucos, and San Simeon Beach State Park, and Fort Bragg and Trinidad Head in northern California. It was found in three different habitats with no apparent correlation with geographical location. This species was found in burrows in (1) the shells of *Tegula brunnea* Philippi inhabited by *Pagurus granosimanus* (Stimpson) (10 specimens at 3 stations), (2) shells of *Pododesmus machroschisma* (Deshayes) (6 specimens at 2 stations at Morro Bay), and (3) in low encrusting coralline algae of the genus *Lithothamnion* (11 specimens at 3 stations). Other polydorids found associated with *Boccardia berkeleyorum* include *B. columbiana*, *B. tricuspa*, and *Polydora* near *ciliata* in *Tegula*; *B. columbiana* and *B. tricuspa* in *Lithothamnion*; and *Polydora* sp. and *P. giardi* in *Pododesmus*. Other *Boccardia* were not found with it in *Pododesmus* material.

***Boccardia chilensis*, new species**

Figure 3

Boccardia sp. Hartman, 1948.

Polydora polybranchia Fauvel, 1916; *Not* Haswell, 1885.

Material examined: Chile, Lund University Chile Expedition 1948-49; Sta. 22, July 16, 1948, Golfo de Ancud, Isla Quenu, Punta Pinto, western side, sheltered intertidal, Lat. 41°49'15" S, Long. 73°10'15" W (2 fragments); Sta. M-121, June 9, 1949, Bahía San Vicente, Punta Liles just W. of San Vicente, semi-exposed intertidal, rocky, Lat. 36°43'36" S, Long. 73°08'10" W (3 specimens—HOLOTYPE and 2 PARATYPES); Sta. 131, July 1, 1949, Iquique, southern part of town, exposed rocky

intertidal, Lat. 20°13'10" S, Long. 70°10'19" W (1); Sta. M-133, July 7, 1949, Iquique, the harbor, sheltered rocky intertidal, Lat. 20°12'30" S, Long. 70°10'19" W (2); Bahía de Concepcion, central part, SE of Isla Quiriquina soft bottom trawl, depth 20 m, Lat. 36°40'15" S, Long. 73°01'48" W (1).

The holotype and 2 paratypes are deposited in the Swedish National Museum, Stockholm.

Description: Of the 9 specimens available for study the 3 types are well-preserved and adequately show diagnostic characteristics. The remaining specimens are poorly preserved and show clearly only the setal characteristics. The holotype is 28 mm long and has 125 segments. There is no body pigmentation.

The prostomium is bifid on its anterior margin and gradually narrows posteriorly to a point near the palpal insertions (Fig. 3a). An enlarged and raised area at about the level of the palpal insertions bears a nuchal tentacle (Fig. 3a). The caruncle extends to the posterior of setiger 2. An enlarged dorsal ridge occurs on some specimens from the anterior border of setiger 5 to near the posterior border of 6. Palps were missing on all specimens and were presumably lost at the time of preservation. There are no eyes.

Setiger 1 has capillary setae in both the noto- and neuropodia. Setigers 2, 3, 4, -, 6 and succeeding setigers have spreading fascicles of winged capillary notosetae arranged in 2 rows. The posterior row has longer and thinner setae. The number of these setae and the distinction between rows rapidly decreases on more posterior setigers. In far posterior setigers only a few laterally directed long capillary setae remain. The neuropodia of setigers 2, 3, 4, -, 6 have fascicles of winged capillary setae. Bidentate hooded hooks begin on setiger 7. Initially, there are up to 16 hooks per fascicle with the main fang of these hooks almost at a right angle to the shaft (Fig. 3g). In far posterior setigers the main fang is strongly bent and forms an acute angle with the shaft (Fig. 3h). In those setigers the hooks number only 8 or 9 per fascicle.

Setiger 5 is large and well-developed (Fig. 3a). There are two types of heavy spines arranged in a curved double row. The dorsally placed setae are simple falcate hooks with a hump at the point of curvature on the convex side (Fig. 3b). The ventral spines have a distal concavity from which arises a small cone (Fig. 3 c-f). The end of the shaft contains randomly dispersed fine "hairs". In certain views one side of the concavity is seen to be elevated as a delicate, transparent rim (Fig. 3 e-f). A small tuft of capillary setae occurs ventral to the major spines.

Branchiae are fingerlike and occur on 2, 3, 4, -, 6 and succeeding setigers and continue to the poste-

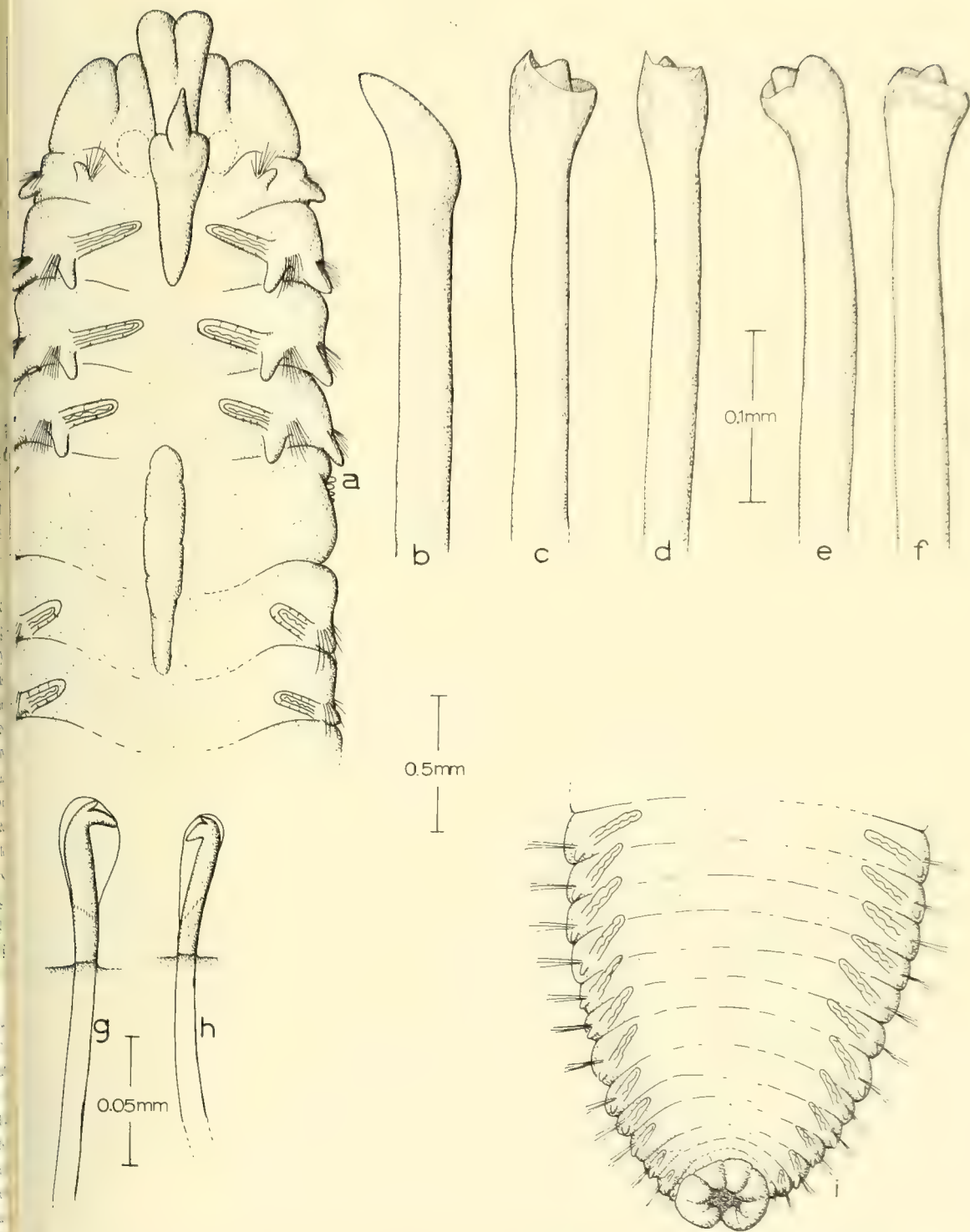


Figure 3. *Boccardia chilensis* new species: a, anterior end in dorsal view; b, humped falcate spines from setiger 5; c-f, spines from setiger 5 with distal concavity; g, hooded hook from setiger 12; h, hooded hook from a far posterior setiger; i, posterior end in dorsal view.

TABLE I. Some Taxonomic Characteristics of the Known Species of *Boccardia*

Species of <i>Boccardia</i>	Prostomial nuchal ridge a. prostomium b. caruncle c. eyes	Branchial distribution a. anterior b. posterior	Notosetae on Setiger 1	Posterior Notopodial Spines	Spines of Setiger 5 a. number of types b. description of types	Pygidium	Other Features	References
<i>basilaria</i>	a. incised b. to end of setiger 3 c. 4	a. 2, 3, 4, -, 6 b. absent posterior one-half	absent	absent	a. two b. 1. falcate 2. bristle- topped with constricted neck	semi- circular disc, with 2 ventral lappets	a. pouched glands in neuropodia of setigers 10-17 b. hooded hooks unidentate in posterior setigers	Hartman (1961; 1969)
<i>berkeleyorum</i>	a. rounded b. to end of setiger 4 c. 0	a. 2, 3, 4, -, 6 b. absent posterior one-fourth	absent	acicular	a. two b. 1. falcate 2. bristle- topped with accessary tooth	four small lobes	bores in calcareous materials	This paper
<i>chilensis</i>	a. incised b. into setiger 2 c. 0	a. 2, 3, 4, -, 6 b. present	present	absent	a. two b. 1. falcate 2. distal concavity	simple weakly lobed collar, ventrally incised	a. nuchal tentacle present b. up to 16 hooded hooks per neuropodium	This paper
<i>columbiana</i>	a. rounded b. to end of setiger 3 c. 4	a. 2, 3, 4, -, 6 b. absent last few setigers	long capillaries present in spreading fascicle	absent	a. two b. 1. falcate 2. bristle- topped	four equal lobes	—	Berkeley (1927) Woodwick (1963a)
<i>hamata</i>	a. incised b. to end of setiger 3 c. 4	a. 2, 3, -, -, 6 b. absent posterior one-fourth	absent	long falcate recurved hooks	a. one b. simple falcate	small ring with 2 ventral blade- like lappets each with a terminal process	dorso-median channel between posterior notopodia	Blake (1966)
<i>ligerica</i>	a. weakly incised b. to end of setiger 2 c. 4	a. 2, 3, -, -, -, 7 b. absent posterior two-thirds	absent	long falcate recurved hooks	a. one b. simple falcate	flattened plate with 2 terminal cirri	dorso-median channel between posterior notopodia; inhabits brackish waters	This paper
<i>natrix</i>	a. incised b. to end of setiger 2 c. 4	a. 2, 3, 4, -, 6 b. present	present	absent	a. two b. 1. falcate 2. bristle top with 2 heavy smooth bosses	four lobes	—	Söderström (1920) Hartman (1948)

TABLE I (CONTINUED). Some Taxonomic Characteristics of the Known Species of *Boccardia*

Species of <i>Boccardia</i>	Prostomial nuchal ridge a. prostomium b. caruncle c. eyes	Branchial distribution a. anterior b. posterior	Notosetae on Setiger 1	Posterior Notopodial Spines	Spines of Setiger 5 a. number of types b. description of types	Pygidium	Other Features	References
<i>B. data</i>	a. incised b. into setiger 5 c. 3-6	a. 2, 3, 4, -, 6 b. absent posterior one-third	present	absent	a. two b. 1. falcate 2. bristle top and club-shaped	simple collar with several weak lobes	large forwardly-directed "lateral fans" on ventral side of setigers 1-4	Khlebovitch (1959)
<i>B. hybranchia</i>	a. incised b. to end of setiger 3 c. 6-8	a. 2, 3, 4, -, 6 b. absent posterior one-half	absent	absent	a. two b. 1. falcate 2. inverted, bristle-topped cone with oblique base	disc-like	ventral oral groove to anterior of setiger 3	Carazzi (1893) Mesnil (1896) Fauvel (1927)
<i>B. boscidea</i>	a. rounded b. to end of setiger 3 c. 4	a. 2, 3, 4, -, 6 b. absent last few setigers	present (short)	absent	a. two b. 1. simple falcate 2. bristle-topped	4 lobes dorsal pair smaller than ventral	pigment along prostomium; diverse habitats of shell, sand mud . . .	Hartman (1940; 1941) Woodwick (1963a)
<i>B. donatrix</i>	a. incised b. to end of setiger 2 c. 2	a. 2, 3, 4, -, 6 b. absent posterior one-third	present	absent	a. two b. 1. simple falcate 2. central cone with raised margins	two flattened glandular cushions	palps barred	Day (1961; 1967)
<i>B. truspa</i>	a. rounded b. to end of setiger 3 c. 4	a. 2, 3, 4, -, 6 b. absent posterior two-thirds	absent	absent	a. two b. 1. falcate 2. tricuspid	4 small lobes	bores in calcareous materials	Woodwick (1963b)
<i>B. micata</i>	a. incised b. to end of setiger 2 c. 4	a. 2, 3, 4, -, 6 b. absent posterior one-fifth	absent	absent	a. one b. simple falcate	disc-like with a dorsal gap	—	Hartman (1936; 1969)
<i>B. redeki</i> (status Okuda, 1971)	a. incised b. to end of setiger 3 c. 4	a. 2, 3, -, -, 6 b. absent posterior one-half	absent	?	a. one b. simple falcate	?	nuchal tentacle present	Okuda (1937)

rior end. Anteriorly they are longest on setigers 2, 3, and 4; they are shorter posterior to setiger 5 through the first one-third of the body and then are more elongate on succeeding segments with another gradual decrease in size near the pygidium.

The pygidium consists of a simple collar with a ventral incision or notch and further subdivision into several weakly developed lobes (Fig. 3i).

Remarks: The species is closely related to *B. tricuspa* (Hartman) and *B. pseudonatrix* Day. It is separated from those species and others of the genus by the characteristics listed in Table I. Fauvel (1916) reported *Polydora polybranchia* from the Falkland Island. His descriptions and figures are, however, clearly those of *B. chilensis*. Two figures show the anterior end with a nuchal tentacle and another figure shows the characteristic spines of setiger 5.

Ecology and distribution: The species was collected both intertidally and subtidally along the coast of Chile. In the intertidal it occurred both in protected and exposed rocky habitats.

KEY TO THE KNOWN SPECIES OF *BOCCARDIA* CARAZZI

- 1a Heavy spines of setiger 5 of one type, simple, falcate 2
- 1b Heavy spines of setiger 5 of two types, first type simple, falcate; second type highly modified 5
- 2a Nuchal tentacle present *B. sp.*
- 2b Nuchal tentacle absent 3
- 3a Recurved posterior spines present; pygidium with lappets or cirri 4
- 3b Recurved posterior spines absent; pygidium saucer-shaped *B. truncata*
- 4a Pygidium with 2 broad ventral lappets, each with a short process ... *B. hamata*
- 4b Pygidium with 2 long anal cirri ... *B. ligerica*
- 5a Second type of heavy spine of setiger 5 with dense bristles on the top 8
- 5b Second type of heavy spine of setiger 5 without dense bristles 6
- 6a Heavy spines of setiger 5 — falcate and tridentate; prostomium rounded ... *B. tricuspa*
- 6b Heavy spines of setiger 5 — falcate and with a distal concavity from which a cone or tooth arises; prostomium incised ... 7
- 7a Nuchal tentacle present; hooded hooks number up to 16 per neuropodium *B. chilensis*
- 7b Nuchal tentacle absent; hooded hooks number only 6 per neuropodium *B. pseudonatrix*

- 8a Prostomium rounded 9
- 8b Prostomium incised 11
- 9a Posterior acicular spines present; bristle-topped spines of setiger 5 with an accessory tooth; notosetae absent from setiger 1 *B. berkeleyorum*
- 9b Posterior acicular spines absent; no tooth on bristle-topped spines of setiger 5; notosetae present on setiger 1 10
- 10a Notosetae of setiger 1 long and in a fan-shaped fascicle *B. columbiana*
- 10b Notosetae of setiger 1 short ... *B. proboscidea*
- 11a Hooded hooks bidentate in anterior setigers, unidentate in posterior setigers; pygidium with 2 ventral lappets *B. basilaria*
- 11b Hooded hooks bidentate throughout; pygidium otherwise 12
- 12a Large forwardly directed lateral pouches on the ventral side of setigers 1-4 *B. perata*
- 12b Lateral pouches absent 13
- 13a Bristle-topped setae of setiger 5 with 2 heavy smooth bosses; notosetae present on setiger 1 *B. natrix*
- 13b Bristle-topped setae of setiger 5 with a conical tip with the bristles continued basally below the thickest region; notosetae absent on setiger 1 *B. polybranchia*

DISCUSSION

As discussed by Woodwick (1964: 156) "The generic breakdown of the polydorid forms has been unstable since the late 1800's and at the present time no one arrangement is accepted by all workers." According to Woodwick's scheme the polydorids may be divided into four genera: *Polydora sensu stricto*, *Pseudopolydora*, *Tripolydora* and *Boccardia*.

Fourteen species of the genus *Boccardia* are here considered valid. Their characteristics are compared in Table I and the species are delineated in the key. *Boccardia* sp. is an unnamed Japanese species [= *B. redeki sensu* Okuda, 1937]. The 14 species may be conveniently arranged into two natural groups based primarily on the setae of setiger 5. The groups are as follows:

I. Superior dorsal fascicle *present* on setiger 5; Spines of setiger 5 of *one* kind, simple and falcate.

B. hamata *B. truncata*

B. ligerica *B. sp.* [= *redeki sensu* Okuda, 1937]

II. Superior dorsal fascicle *absent* on setiger 5; Spines of setiger 5 of two kinds.

a. One spine simple falcate and second with one or more projecting cusps.

B. chilensis *B. tricuspa*

B. pseudonatrix

b. One spine simple falcate and second bristle-topped.

B. basilaria *B. perata*

B. berkeleyorum *B. polybranchia*

B. columbiana *B. proboscidea*

B. natrix

Two species of Group I (*ligerica* and *hamata*) have recurved posterior spines, while one species in Group II b (*berkeleyorum*) has acicular posterior spines.

Several species of the polydorid complex possess posterior notopodial spines. In some cases the species may be closely related but in others not, and their specialization in structure then suggests convergent evolution. *Polydora hoplura* Claparède and *P. colonia* Moore have recurved posterior spines similar to those of *Boccardia ligerica* and *hamata*, however the adult, and quite importantly, the larval morphologies are different in the four species. Posterior spines are such important diagnostic characteristics it would be helpful to learn more about their relation to the ecology of the respective species. Other polydorids known to have posterior spines include; *Polydora caulleryi* Mesnil, *P. quadrilobata* Jacobi, *P. armata* Langerhans, *P. cardalia* Berkeley, *P. caeca* Oersted, *Pseudopolydora corallicola* Woodwick and *Tripolydora spinosa* Woodwick.

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PARASITIC MITES OF SURINAM. VIII. A NEW GENUS AND SPECIES OF CHIGGER, *FAURANIUS ATECMARTUS*, AND ADDITIONAL RECORDS OF SPECIES (ACARINA: TROMBICULIDAE)¹

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ABSTRACT: Twenty-six species of chiggers are now known from Surinam. Nineteen are recorded here. *Fauranius* new genus is described for *F. atecmartus*, new species off *Philander opossum* and *F. myoproctae* (Fauran, 1960), new combination.

This paper augments a recent report (Brennan, 1970) in which 11 species of chiggers are recorded from Surinam. Fifteen additional species, one new, are recorded here. All material was collected by the junior author.

Two specimens of each species, as available, will be deposited in Rijksmuseum van Natuurlijke Historie, Leiden, The Netherlands, and National Collection of Surinam, Centraal Laboratorium, Paramaribo.

Fauranius, new genus

Type species: *Fauranius atecmartus*, new species. Neotropical trombiculine larvae. Leg segmen-

tation 6-6-6 (unique in subfamily Trombiculinae); 2 genualae I, sub- and parasubterminala, microtarsala I proximad of tarsala I, no genuala II and III, a tibiala III, no mastisetae. Scutum wider than long, the posterolateral setae extrascutal, sensillae probably expanded (as suggested by remaining stubs). Apparently, eyes may be present or absent.

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Cheliceral blade with tricuspid cap. Galeal seta nude. Palpal tibial claw trifurcate, palpal tarsus with 5 branched setae and a tarsala.

Distinguished from *Pseudoschoengastia* by leg segmentation 6-6-6 and absence of setae between coxae II and III. Referred species: *Pseudoschoengastia myoproctae* Fauran, 1960.

Fauranius is named for Dr. Pierre Fauran, Pasteur Institute of French Guiana, who has made significant contributions to the knowledge of neotropical chiggers.

***Fauranius atecmartus*, new species**

Type data: Holotype and 2 paratypes, RML 55406, from ears of *Philander opossum*, Coronie, Surinam, 28 November 1969, F. Lukoschus.

Holotype to be deposited in Rijksmuseum van Natuurlijke Historie, Leiden; paratypes in the Rocky Mountain Laboratory.

Diagnosis: Leg segmentation 6-6-6. Extrascutal posterolateral setae; less than 30 dorsal setae; no genuala II and III, no mastisetae, microtarsala I proximad of tarsala I. Distinguished from *F. myoproctae* by differently shaped scutum, $PL > AM$, smaller leg index because of shorter leg II, smaller tarsalae I and II, and microtarsala I much closer to tarsala I.

Body: A small chigger, broad-ellipsoidal when engorged. Eyes not discernible. Anus at sixth row of ventral setae. Length and width of holotype, nearly engorged, 335 by 260 μ .

Gnathosoma: Sparsely punctate. Cheliceral blades with small tricuspid cap. Galeal seta nude. Palpal setae sparsely branched, B/B/BNB, tarsus 5B and a tarsala, tibial claw trifurcate.

Scutum: As figured, lightly punctate; sensillae broken off in all specimens, but in one the remaining stubs are suggestive of expanded heads; extrascutal $PL > AM > AL$. Scutal measurements of holotype; AW 47, SB 32, ASB 18, PSB 17, AM 27, AL 18, PL 34.

Legs: Segmentation 6-6-6. Lightly punctate, specialized setae as figured; 2 genualae I, sub- and paraterminala, no genuala II and III, a tibiala III, no mastisetae, microtarsala I proximad of tarsala I. Nonspecialized setae sparsely branched. Coxal III seta slightly anterior of center.

Body setae: Dorsal setae; humerals 34 μ , dorsals 25 to 31 μ , arranged 2-6-6-6-4-4 (holotype), 2-6-6-6-4-2 (a paratype). Ventral setae 2-2 plus 36; postanals, paranals, and preanals of last 2 rows similar in form to dorsals.

Remarks: Fauran (1960) described *Pseudoschoengastia myoproctae* in detail from a single specimen attached to teat of *Myoprocta acouchy*, Moy-



Figure 1. *Fauranius atecmartus*. Scutum and specialized setae of legs with measurements in microns.

enne-Mana, French Guiana, April 1960. He noted the unique 6-6-6 leg segmentation. Geest and Loomis (1968) saw the holotype and retained the species in *Pseudoschoengastia* in their "Aeci Group".

Although we have not seen the holotype, it is clear from the description that *F. myoproctae* and *F. atecmartus* are closely related. Both are small, with corresponding small structures. Certain characteristics of *F. myoproctae* and *F. atecmartus*, respectively, are: leg index 570 and 519; dorsal formula 2-6-6-6-6-2-2 and 2-6-6-6-4-4; length of humeral setae 35 μ and 34 μ ; length of other dorsals 20 to 29 μ and 25 to 31 μ ; eyes distinct 2/2 and eyes not discernible; lengths of tarsalae I and II 18 μ , 17 μ and 14 μ , 12 μ .

Crotiscus desdentatus tissoti Fauran, 1960

Six specimens off *Proechimys guyannensis*, Lelydorp, 18 December 1969.

Euschoengastia (s. l.) *desmodus* (Brennan and Dalmat, 1960)

Two larvae from ventral wing membrane of *Glossophaga soricina*, Brownsweig, 9 February 1970; 1 off *Carollia perspicillata*, Onverwacht, 5 February 1970.

This bat chigger and a new species from Venezuela are being referred to a new genus in a subsequent paper.

Eutrombicula alfreddugesi (Oudemans, 1910)

Five larvae off *Proechimys guyannensis*, Lelydorp, 18 December 1969; 3 off *P. guyannensis*, Uitkijk, 8 January 1970; 3 off 3 *Didelphis marsupialis*, Coronie, 29 November 1969 to 12 February 1970; 1 off *D. marsupialis*, Brokobaka, 21 February 1970; 2 off *Philander opossum*, Coronie, 10 January 1970; 6 off *Rattus rattus frugivorus*, Brokobaka, 21 February 1970; 4 off *Nectomys squamipes melanius*, Coronie, 12 February 1970.

Eutrombicula batatas (Linnaeus, 1758)

Six larvae from ears of 3 *Rattus norvegicus*, Paramaribo, 13 and 15 January 1970; 2 from ears of *Herpestes auropunctatus*, Meerzorg, 3 March 1970; 1 from ears of *Tamandua tetradactyla*, Lelydorp, 17 December 1969; 1 from scrotum of *Eptesicus melanopterus*, Meerzorg, 3 March 1970.

This Linnaean species, the oldest recorded trombiculid mite, the "sweet potato chigger," is recorded again from the country of its discovery. For details concerning the history, biology and systematics of *Eutrombicula batatas* see Michener (1946), Jenkins (1949), and Fuller (1952).

Eutrombicula goeldii (Oudemans, 1910)

Three specimens off *Proechimys guyannensis*, Lelydorp, 18 December 1969; 2 off *Didelphis marsupialis*, Coronie, 12 February 1970; 2 off *Epicrates cenchris* (rainbow boa), Brokopondo, 2 February 1970; 3 off *Psarocolius decumanus*, Lelydorp, 23 January 1970.

Eutrombicula tinami (Oudemans, 1910)

Two larvae off *Didelphis marsupialis*, Brokobaka, 21 February 1970.

This form has not been recorded since it was described off Tinamou, Brazil. It is very close to, and may indeed prove to be *Eutrombicula goeldii* with branched palpogenua and palpoventrotibial setae.

An additional record is 5 specimens off *Proechimys semispinosus*, Galeta Point, Panama, 23 February 1950.

Microtrombicula fragibarba
(Brennan and Jones, 1960)

Eight larvae from ears of *Didelphis marsupialis*, Brokobaka, 21 February 1970; 7 off 2 *D. marsupialis*, Coronie, 29 November and 4 December 1969; 7 off *D. marsupialis*, Lelydorp, 12 January 1970; 1 off *D. marsupialis*, Paramaribo, 31 January 1970; 1 off *Philander opossum*, Coronie, 10 January 1970.

Microtrombicula nr. *tragulata*
(Brennan and Jones, 1961)

Six larvae off *Didelphis marsupialis*, Brokobaka, 21 February 1970.

Nasicola annereauxi Brennan and Yunker, 1969

Twenty-six larvae from nasal passages of *Noctilio labialis*, Lelydorp, 23 January 1970; 43 from 3 *N. labialis*, Meerzorg, 2 March 1970.

This intranasal chigger of bats described from *Phyllostomus hastatus*, Venezuela is also known from *P. hastatus* and *N. labialis*, Colombia.

Odontacarus tubercularis (Brennan, 1952)

Seven larvae off *Proechimys guyannensis*, Uitkijk, 8 January 1970; 1 off *Philander opossum*, Coronie, 28 November 1969; 2 off *P. opossum*, Coronie, 12 February 1970; 1 off *Nectomys squamipes melanius*, Coronie, 12 February 1970.

Parasecia aitkeni (Brennan and Jones, 1960)

Four specimens off *Philander opossum*, Coronie, 10 January 1970.

Parasecia manuli (Brennan and Jones, 1960)

One larva off *Proechimys guyannensis*, Uitkijk, 8 January 1970; 2 off *P. guyannensis*, Lelydorp, 18 December 1969; 12 off 4 *Philander opossum*, Coronie, 28 November 1969 to 12 January 1970; 4 off 3 *Didelphis marsupialis*, 29 November 1969 to 12 February 1970.

Parasecia valida (Brennan, 1969)

Two larvae off *Proechimys guyannensis*, Lelydorp, 18 December 1969.

Perissopalla barticonycteris Brennan, 1969

Five larvae off 2 *Carollia perspicillata*, Brownsweg, 10 February 1970.

Perissopalla ipeani Brennan, 1969

Six larvae off 3 *Carollia perspicillata*, Onverwacht, 5 February 1970.

Quadreseta flochi (Brennan and Jones, 1960)

Two larvae off *Proechimys guyannensis*, Uitkijk, 8 January 1970.

Speleocola secunda Brennan and Jones, 1960

Three larvae off *Carollia perspicillata*, Zandery, 7 January 1970; 1 from ventral wing membrane of *Saccopteryx bilineata*, Lelydorp, 26 February 1970.

Tecomatlana (Hooperella) vesperuginis
(Brennan and Jones, 1960)

Thirteen larvae off 2 *Carollia perspicillata*, Zandery, 7 January and 1 February 1970; 2 off *C. perspicillata*, Brownsweig, 10 February 1970; 2 from wing membrane of *Saccolpteryx bilineata*, Lelydorp, 26 February 1970; 6 from ventral wing membrane of 3 *Glossophaga soricina*, Brokopondo, 2 February 1970.

The following chiggers of Surinam, not listed here, were recorded recently by Brennan (1970).

Arisocerus amapensis Brennan, 1970

Boshkerria punctata (Boshell and Kerr, 1942)

Colicus icomi Brennan, 1970

Colicus oblonga (Fauran, 1959)

Eutrombicula alfreddugesi (Oudemans, 1910),
tropica form of Ewing, 1925

Pseudoschoengastia tricola (Brennan and Jones, 1961)

Tecomatlana (Hooperella) saccolpteryx (Brennan and Jones, 1960)

Trombicula (s. l.) *palmigera* Fauran, 1960

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VARIATION AND GEOGRAPHIC DISTRIBUTION IN SOME ARGENTINE AND CHILEAN OSMYLIDAE, WITH A NEW SPECIES OF *KEMPYNUS* (NEUROPTERA).

PHILLIP A. ADAMS¹

ABSTRACT: A similar color variation, which consists in longitudinally streaked wings, occurs in *Kempynus falcatus* Navás and *Phymatosmylus caprorum* Adams. These species are sympatric with the newly described *Kempynus crenatus* on the western slope of the Andes between 34°30' S and 40° S, but further south in Chiloé and Aysén, *K. falcatus* occurs on the coast.

The material discussed below was not available for inclusion in my recent paper on South American Osmylidae (Adams, 1969). *Kempynus* is of particular interest because it includes species from Australia-New Zealand and South American (Kimmins, 1940). I am grateful to Ellis MacLeod of the University of Illinois, Urbana, for the loan of specimens and for helpful comments.

Description: Head pale with the following fuscous marks: dark border of antennal sockets confluent with large frontoclypeal triangle which has apex at anterior clypeal margin, spots anterior to anterior tentorial pits, borders of ocelli and vertex scars. Mouthparts fuscous, antennae pale. Pronotum pale, dark dotted, four black spots on transverse furrow. Mesonotum pale, dark-punctate, prescutum with

***Kempynus crenatus*, new species**

Figures 1; 2A, C, E-H

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Figure 1. *Kempynus crenatus*, wing venation.

four dark marks, black triangle on prescutal-scutal suture, scutum and scutellum black laterally. Pleurae irregularly variegated, coxae fuscous, fore and mid-femora with pair of subapical central dark marks and dark dorsoapical spot, hind femora paler. Tibiae pale, dark bands at base, middle and apex. Tarsi brownish, apical tarsomere dark. Female fore coxa with an anterolateral field of numerous short pedestalled setae. Wing venation as in Figure 1. MP2 of forewing dichotomously branched basad of union of CuA and CuP, posterior fork pectinate. Malculations brown.

Abdomen fuscous at tip; setal bases infusate. External male abdominal apex much as in *K. incisus* (Kimmins, 1940). Gonocoxites (Fig. 2A) resemble those of *K. falcatus* (Fig. 2B), but are more elongate. Hypandrium internum (Fig. 2C) more elongate than in *K. falcatus*. Female abdominal apex much as in *K. falcatus*, eighth sternite (Fig. 2F, G) setose anterolaterally, posterior lobes shorter and more rounded than in *falcatus*. Spermathecae slightly bent, constricted in middle, basal portion spherical; in one specimen, the spermathecae are ovoid (Fig. 2E). Colleterial gland reservoir (Fig. 2H, cgr) and

bulb slightly longer than in *falcatus*, and bursal gland duct (bgd) less tortuous.

Measurements (mm). Forewing length, ♀, 28.0, 28.5, 29.0; ♂ 26.0. Antenna length, ♀, 7.0, 8.0, 8.3; ♂ 7.5.

Holotype. Chile, Prov. Ñuble, Cordilleras Chila, Las Trancas, 12 km E. Recinto, 1-10 Dec. 1964, ♀, leg. L. E. Peña, Museum of Comparative Zoology, Harvard [ca. 800 mt., 71°37' W, 36°51' S].

Allotype. Argentina, Prov. Neuquén, Pucará, Parque Nacional Lanín, Jan. 1951, ♂, leg. S. S. Schajovskoy, Museum of Comparative Zoology, Harvard (ex coll. E. G. MacLeod).

Paratypes. 1 ♀, same data as holotype, E. G. MacLeod collection. Argentina, Prov. Neuquén, Pucará, 30 Nov. 1959, ♀, purch. ex F. H. Walz, P. Adams collection.

Remarks. This species differs from *falcatus* in its oval wing shape, and shape of spermathecae. In *K. longipennis*, the wings are similarly shaped, but the wingtips are somewhat more acute, MP2 forks pectinately, and the marginal pale areas of *K. crenatus* are absent. In all the other species of

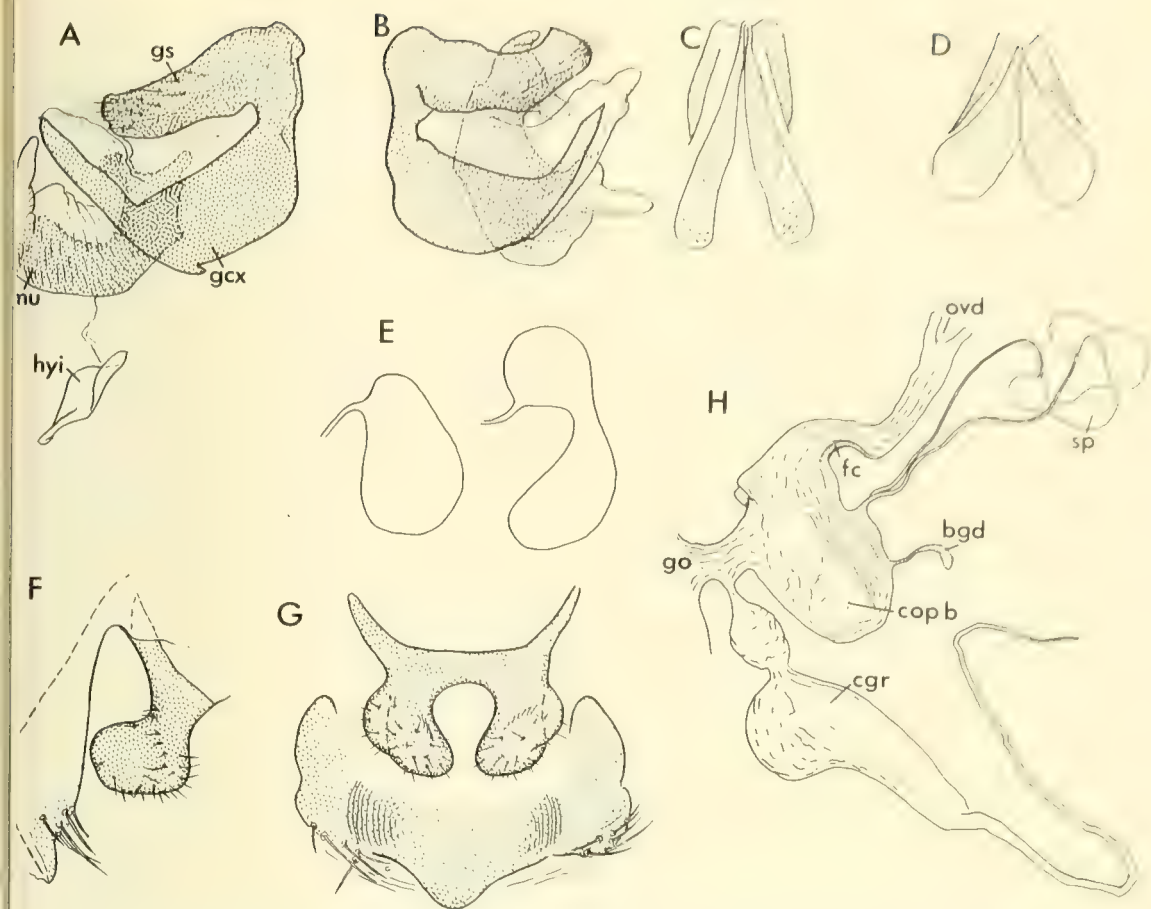


Figure 2. Reproductive structures. A, C, E-H, *Kempynus crenatus*. B, D, *K. falcatus*. A, B, genital armatures of males, lateral view. C, D, hypandrium internum. E, spermathecae. F, eighth abdominal sternite of female, lateral view. G, same, ventral view. H, female reproductive system viewed from the left side, abdominal apex downward.



Figure 3. Striped wing pattern: A, *Phymatosmylus caprorum*; B, *Kempynus falcatus*.

Kempynus the apical projections of the female eighth sternite are more slender and more separated basally.

Kempynus falcatus Navás

Figures 2B, D; 3B

Kempynus falcatus Navás 1912, 1928, 1930, 1936, Kimmins, 1949. Type: ♀, Chile, Mulchen [Bio Bio, 37° 44' S, 72° 15' W], Jan. 1902, leg. H.J. Elwes, Brit. Mus. (Nat. Hist.), not seen.

Kalosmylus falcatus, Krüger, 1913, 1914.

Remarks. The male genitalia have not previously been described. As Kimmins (1940) noted, these are similar in most species of *Kempyninae*, and reference to Fig. 2B demonstrates that *K. falcatus* constitutes no exception. Most of the apparent differences from *K. crenatus* are due to positioning. However, the hypandrium internum (Fig. 2D) is broader, with the winglike lobes fused on the midline, while they are separate to the base in *K. crenatus*.

Distribution. The following specimens, unless

otherwise noted, are in my collection and were collected by L. E. Peña. *Chile*: Curicó, Buchén, Mar. 1956, ♀, ("farm in preandean foothills"); Curicó, La Jaula (Los Queñes), Andes, 14-18 Feb. 1965, ♂; Linares, Fundo Malcho ("in the high mountains") Dec. 1952, ♀; Malleco Prov., Termas de Tolguaca, 30 km NE Curacautin, 20 Jan. 1959, ♂; Cautin 30 km N Villarica, 1-30 Jan. 1965, 6 ♂ 4 ♀; Chiloé, Dalcahue, Feb. 1954, ♂; Aysén, Pto. Cisnes, Feb. 1961, ♀; Aysén, Rio Maniguales [vic. Puerto Aisén] 27 Jan. 1961, 1♂, 1♀. *Argentina*, Neuquén, Pucará, Parque Nacional Lanín: 31 Nov. 1959, ♀, purch. ex. F. H. Walz; Feb. 1951, ♀, Feb. 1952, ♂, leg. S. S. Schajovskoy, E. G. MacLeod collection.

Color variation. In my collection are single specimens of *Phymatosmylus caprorum* Adams (Fig. 3A ♀, from Las Trancas, Cord. Chillan, Chile, 1-10 Jan. 1964, L. E. Peña leg.) and *Kempynus falcatus* Navás (Fig. 3B, ♀, 30 km N. Villarica, Prov. Cautín, Chile, 1-30 Jan. 1965, L. E. Peña leg.) which have a dark stripe on each wing instead of the usual mottling. While similar color patterns are common in other Neuroptera (e.g. the poly-stoechotids *Platystoechotes* and *Fontecilla*, and many Myrmeleontidae) they do not ordinarily occur in related Osmyliidae (Kimmins, 1940). The capacity to develop similar aberrant color patterns may suggest a closer relationship between these osmyliids than indicated by their present taxonomic position. They are now placed in different subfamilies (*Phymatosmylus* in *Stenosmylinae*, *Kempynus* in *Kempyninae*) although *Phymatosmylus* is regarded as transitional toward *Kempyninae* (Adams, 1969).

Geographic distribution (Fig. 4). *Kempynus falcatus*, *K. crenatus*, and *Phymatosmylus caprorum* are sympatric along the western slope of the Andes, from about 34° 30' S to 40° S, extending into Argentina in the lake region, where several passes exist at 1200m elevation. All three species have been taken at Pucará, Lanín National Park, Argentina. Further south, in Chiloé and Aysén, the much commoner *K. falcatus* occurs on the coast, an elevational shift probably related to the cooler climate. Also plotted are localities for *K. falcatus* from Kimmins (1940) and from Navás (1928, 1930).

None of these species appears to be sympatric with *Isostenosmylus*, which has several species in Ecuador, Peru, Bolivia, and Brazil, or with *Paryphosmylus*, with one species in Ecuador.

Seasonal abundance. Combined data from 50 specimens of the three species indicate greatest frequency of capture near the time of the December solstice: November — 7, December — 21, January — 15, February — 6, March — 1.

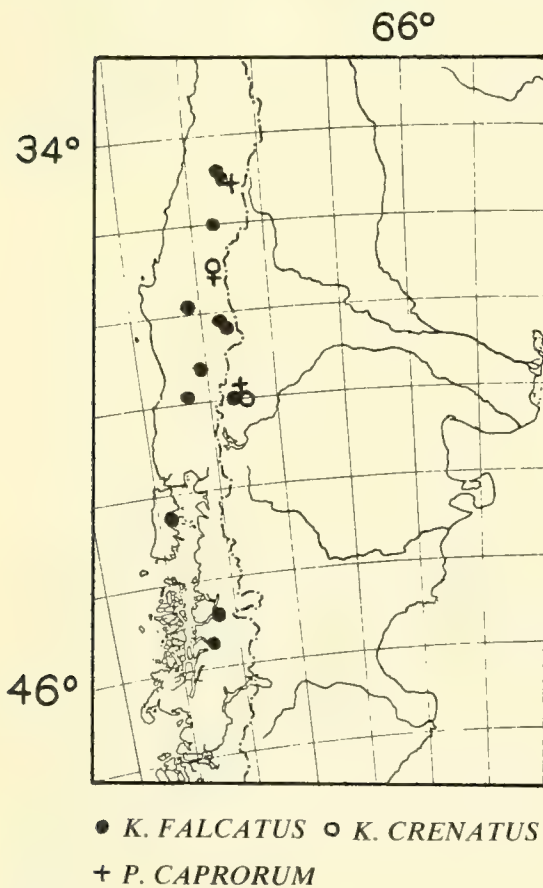


Figure 4. Known distribution of South American Kempyninae and Stenosmylinae.

ABBREVIATIONS

Bcd — bursal gland duct, cgr — colleterial gland reservoir, cop b — copulatory bursa, CuA — cubitus anterior, CuP — cubitus posterior, fc — fertilization canal, gcx — gonocoxite, go — genital opening, gs — gonarcus, hyi — hypandrium internum, MP — media posterior, mu — medianus, ovd — oviduct, sp — spermatheca.

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RESEARCH NOTES

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DISTRIBUTION OF SOME SOUTHERN CALIFORNIA KANGAROO RATS

The ranges illustrated by Grinnell (1922) and Hall and Kelson (1959) for southern California kangaroo rats were drawn by encircling known records of occurrence in the latter case without regard to physiography or habitat. While collecting specimens of *Dipodomys agilis*, *D. panamintinus*, and *D. microps* for a recent study (Csuti, 1969), it became apparent that the published ranges of these species in southern California were inaccurate. Conventional museum study skins were prepared from all specimens examined and are deposited in the collection of the Natural History Museum of Los Angeles County (LACM) unless otherwise noted. Plant communities referred to are those described by Munz and Keck (1959).

Dipodomys panamintinus mohavensis (Grinnell). — Eleven specimens were taken from Soledad Canyon in the upper Santa Clara River valley (Los Angeles County). These specimens, captured in Pinyon-Juniper Woodland habitat, are from an area formerly indicated (Hall and Kelson, 1959) to be within the exclusive range of *D. agilis agilis*. A specimen of *D. panamintinus* (San Fernando Valley State College Vertebrate Collection [SFVSC] 746) was taken from Rye Canyon, near Castaic Junction, in similar habitat farther down the Santa Clara River valley. It appears that the presence of Pinyon-Juniper Woodland habitat along this river valley has allowed the penetration of *D. panamintinus* westward into the San Gabriel Mountains from the Antelope Valley for a distance of at least 28 miles.

Dipodomys microps microps (Merriam). — Two specimens (LACM 28342, SFVSC 861) were taken 6 miles north of Lancaster, Los Angeles County, in Alkali Sink habitat. This locality extends the known range of this species 50 miles west of the isolated population previously reported from Victorville by Grinnell (1922). The habitat at the Lancaster locality is typical for this race in its northern range in Owens Valley, since it is "dry sandy ground, sparsely grown to desert shrubbery such as salt-bush" (Grinnell, 1933: 164). *Dipodomys microps* probably has a discontinuous distribution in the Antelope Valley composed of relict populations in those low-lying areas where the Alkali Sink habitat persists.

Dipodomys agilis perplexus (Merriam). — Vaughan (1954) has taken 17 specimens of this kangaroo rat in the eastern San Gabriel Mountains.

Hall and Kelson (1959) indicated a connection between the populations represented by these specimens and those previously known from the Tehachapi Mountains. Since *D. a. agilis* occurs at Elizabeth Lake (Hall and Kelson, 1959) on the interface of the San Gabriel Mountains and the Antelope Valley, any connection between the two *D. a. perplexus* populations must lie to the north of this locality (as illustrated by Hall and Kelson, 1959) and is necessarily confined to a path across the floor of the Antelope Valley. *Dipodomys agilis perplexus* typically occupies Sagebrush Scrub habitat at higher elevations (Vaughan, 1954), and is nowhere reported from desert areas. The absence of any suitable habitat in the Antelope Valley, together with the absence of specimens from intervening areas, makes it appear unlikely that a connection exists between the populations in the Tehachapi and the eastern San Gabriel Mountains. The populations of *D. a. perplexus* in the eastern San Gabriel Mountains seem to be ecologically distinct from *D. a. agilis*, according to Vaughan (1954). These populations may represent an isolated segment of the currently named *D. a. perplexus* which was formerly connected with the Tehachapi Mountains population, but due to a change in habitat is now restricted to the higher elevations of the eastern San Gabriel Mountains. Alternatively, the specimens in question may represent a population derived from *D. a. agilis* which adapted to a habitat similar to that of *D. a. perplexus* of the Tehachapi Mountains, and which responded morphologically to this habitat in a manner parallel to that of *D. a. perplexus*.

These distributional changes emphasize the importance of considering habitat in determining ranges of small mammals. The complex pattern of plant communities in southern California has resulted in a similarly complex pattern of faunal distribution. This requires more than the usual caution when drawing ranges for local animals.

ACKNOWLEDGMENTS

I wish to thank Drs. George F. Fisler and Andrew Starrett for their assistance in this research. Specimens SFVSC 746 and 861 were collected by T. S. Kelly and M. Weigand respectively. This paper is part of a thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at San Fernando Valley State College.

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AN EVALUATION OF TWO METHODS OF MEASURING METACARPAL LENGTH IN *ARTIBEUS LITURATUS* (OLFERS) (CHIROPTERA: PHYLLOSTOMATIDAE).

Two alternate methods are currently employed in measuring metacarpal length of bats. An extensive literature perusal of studies on bats utilizing the measurement of metacarpal length revealed that the method of measuring is seldom stated. Comparative use of the data in such publications is therefore possible only when one has personal knowledge of the investigator and the type of method employed by him in the particular study. The distance measured is from the metacarpal-first phalanx articulation to either 1) the proximal end of the respective metacarpal, or 2) the apex of the wrist joint formed by the summit of the scapholunar. The carpals are therefore excluded in the first (e.g., Starrett and de la Torre, 1964) and included in the second (e.g., Davis, 1970) of the two methods. In either method, the measurement is usually taken between two parallel planes oriented perpendicular to the proximodistal axis of the metacarpal.

Prior to extensive use of either method in a systematic study of the Neotropical bat, *Artibeus lituratus* (Olfers), an attempt was made to determine the greater desirability, if any, of either method. One series of 50 adult specimens (10 males, 40 females) was subjected to both methods of measuring the

length of the second, third, fourth and fifth metacarpals.

The series was obtained during a seven day period, 10 to 17 May 1963, from adjacent sides of the Rio Coco [= Rio Segovia, = Wanks River] which separates Honduras and Nicaragua, at a locality 78 mi. ENEE Danli, Honduras. All specimens are deposited in the Texas Cooperative Wildlife Collection, Texas A & M University

A statistical comparison of both methods is shown in Table 1. The variance-ratio ($F = s^2_1/s^2_2$) was used to test the hypothesis that one method consistently yielded observations with smaller variance and was therefore the more desirable. None of the F-values was significant at the 5 per cent level. The method including the carpals consistently yielded smaller coefficient of variation values but slightly higher variances for the third and fifth metacarpals.

From a statistical point of view, it appears that either method can be employed without introducing significant bias. In practice, however, the method excluding the carpals is subject to greater error because of measuring technique. Determination of the exact proximal end of the respective metacarpals was difficult and time consuming. The topography of the wrist joint varied in study skins depending upon the quality of preparation which further hindered the development of a reasonably rapid, easy and consistent measuring technique. Unless prior usage or specific needs dictate otherwise, I suggest that the method including the carpals is the more satisfactory.

TABLE I. Comparison of two methods of measuring the second, third, fourth and fifth metacarpals (MC) of one series of *Artibeus lituratus*.

EXCLUDING CARPALS				INCLUDING CARPALS			
MC	MEAN	s ² *	CV	MEAN	s ² ₂	CV	F**
	RANGE			RANGE			
2	53.4 48.5-58.8	5.53	4.40	56.5 51.4-61.4	5.29	4.07	1.05
3	64.7 59.0-71.5	5.18	3.52	67.9 62.3-75.0	5.28	3.38	0.98
4	64.0 57.6-69.9	5.97	3.82	66.2 60.0-72.0	5.15	3.43	1.16
5	65.2 59.6-71.6	5.82	3.69	68.5 62.6-75.6	5.87	3.54	0.99

*s² and CV, variance and coefficient of variation, respectively.

**The F-value is obtained from the variance-ratio. s²₁/s²₂. Sample size is 50 throughout; measurements in mm.

ACKNOWLEDGMENTS

Appreciation is extended to Gail Glick for clerical assistance, and to Dilford C. Carter, William B. Davis and Andrew Starrett for suggestions concerning the manuscript. For permission to examine specimens under their curation, I thank William B. Davis and Dilford C. Carter.

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A NEW SYNONYMY IN THE GENUS *CHILICOLA* (Hymenoptera: Colletidae)

Cockerell (1918) described *Prosopis howardiella* from a male specimen taken at Oaxaca, Mexico on April 30 by L. O. Howard. The description is sufficiently detailed to indicate that the bee was not correctly assigned generically.

In 1968 I had the opportunity to examine the type of *Prosopis howardiella*, in the collection of the U. S. National Museum, and found it to belong to the genus *Chilicola*, in the subfamily Chilicolinae. This male is identical to those of *C. ashmeadi* (Crawford, 1906). The type of the latter species is a female, also in the USNM collections. Males have been associated with this name by Eickwort (1967) who reared both sexes in Costa Rica. *Prosopis howardiella* Cockerell, 1918, is clearly a junior synonym of *Chilicola ashmeadi* (Crawford, 1906) (NEW SYNONYMY).

Eickwort recorded a male from Chiapas, Mexico as probably belonging to *C. ashmeadi*. I have seen specimens of both sexes from several localities in Chiapas. I have also seen a male from Antigua, Guatemala and another from Mt. San Salvador, El Salvador.

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Roy R. Snelling, *Natural History Museum of Los Angeles County, Los Angeles, California 90007.*

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CUVIER'S BEAKED WHALE, *ZIPHIUS CAVIROSTRIS*, FROM BARBADOS

On 14 May 1968, Rathjen examined and photographed a beached carcass of a female Cuvier's beaked whale, *Ziphius cavirostris*, at Cattlewash, Walker's Bay, on the northeastern (windward) shore of the Lesser Antillean island of Barbados. The whale was on the beach the day before as noted in the Barbados Advocate — News for 14 May, with one photograph. The condition of the carcass suggested that it had been dead for several days. Color photographs show the body to be moderately dark blue-gray except for a dirty white or light gray lower jaw and upper lip.

Rathjen took several centimeter measurements on the right side as in Norris (1961) and these were: tip of upper jaw to tip of right fluke (flukes were bent so that they were in a perpendicular rather than the normal horizontal plane), 454; tip of lower jaw to tip of left fluke, 470; tip of upper jaw to origin of dorsal fin, 294; origin of dorsal fin to tip of right fluke, 160; tip of dorsal fin to tip of right fluke, 144; origin of flipper to center of posterior edge of flukes, 350; tip of upper jaw to anterior margin of eye, 60; tip of upper jaw to angle of gape, 30; length of flipper, origin to tip, 53; width of base of flipper, 23; width of flukes, tip to tip, 122; depth of flukes from anterior margin to center of posterior edge along axis of body, 37; height of dorsal fin, 18; length of dorsal fin base, 30; length of throat creases, 20; length of eye, 4; height of eye, 1.5.

The carcass was buried by surf action and unfortunately Rathjen was unable to relocate the exact spot for excavation and the record is now limited to several color and black and white photographs and the measurements.

A second *Ziphius*, in slightly fresher condition than the first, stranded on the beach at Bathsheba, St. Joseph, on the northeastern side of Barbados about 5-6 km from the first stranding, on 7 April 1969. Circumstances prevented Rathjen's getting

to the site before the carcass was buried. This carcass was unearched briefly in early June and Rathjen was able to obtain the cranium shortly before the local health authorities insisted on reburying the remains. In early 1970, Joseph C. Moore of the Field Museum of Natural History examined the cranium at the Caldwell's laboratory and noted that it was a female (we had not been able to tell from the carcass photographs, taken at a bad angle) and that it measured 893 mm in condylobasal length.

The closest published western Atlantic records for *Ziphius* are from Argentina to the south (Hershkovitz, 1966) and Puerto Rico to the north (Erdman, 1962).

There are a few records of other cetaceans from Barbados. From specimens obtained in 1869, Turner (1912) listed the mandible of *Globicephalus melas* from Speightstown (probably *Globicephala macrorhyncha*, the only pilot whale now known in the Lesser Antilles) and the mandibles of *Tursiops tursio* (= *T. truncatus*) and of *Prodelphinus* sp. (= *Stenella* sp.) with no locality data other than Barbados. The latter, with a tooth count of 35, probably was one of the spotted dolphins of the *frontalis* group (Fraser, 1950). Brown (1942) listed sperm whales, *Physeter catodon*, and humpback whales, *Megaptera novaeangliae* from off the island.

We wish to thank Dr. Albert Jones who arranged to have the cranium of the second specimen brought to Miami aboard the National Marine Fisheries Service's R/V UNDAUNTED and later transhipped it to the Caldwell's.

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ADDITIONAL SPECIMENS OF THE COLUBRID SNAKE *AMASTRIDIMUM* *VELIFERUM* COPE FROM COSTA RICA. WITH COMMENTS ON A PSEUDOHERMAPHRODITE

A review of the genus *Amastridium* (Wilson and Meyer, 1969) listed six specimens of this rare snake from Costa Rica, all from the Atlantic versant. The locality, San José, given for the holotype of *Fleischmannia obscura* Boettger, the only specimen of *Amastridium veliferum* previously recorded from the Pacific versant of Costa Rica, has been questioned (Scott, 1969). By good fortune, two specimens of definite Pacific versant provenance have since been obtained. One of these (Museo Nacional de Costa Rica, UCR 2819) was taken by Pedro Leon near the airport about 3 km southwest of Rincón, Peninsula de Osa, Puntarenas Province, on 6 August 1969. The other (MNCR 3142) was obtained by Norman J. Scott, Jr. at Finca Las Cruces, 2 km south of San Vito, Puntarenas Province, on 16 March 1969. The first locality is not more than 100 m above sea level, the second approximately 1200 m. The only other known Pacific slope occurrence for the species is in Chiapas, México.

We first examined MNCR 2819 and noted that it is peculiar in a number of respects. Later, one of us (Robinson) located a second Pacific versant specimen which helps to clarify the status of *Amastridium* from this versant. The first specimen (MNCR 2819) is a male with 111 ventrals, the lowest count for the species. Wilson and Meyer (1969) recorded 119 as the lowest ventral count based on a male from southern Nicaragua. This Costa Rican specimen is also the only one known to show dorsal scale row reduction. All specimens examined by Wilson and Meyer have 17 dorsal scale rows throughout the length of the body. The scale reduction pattern of MNCR 2819 is as follows: $17 \frac{2+3}{2+3} \frac{(108)}{(106)} 15$ (111). Furthermore, MNCR 2819 has a single anal plate (there is only a trace

of a groove on the anterior portion of the scale), all other specimens have a divided anal plate. The number of subcaudals in this specimen is 70, 2 less than the lowest count for males from throughout the range (the subcaudal range is 72 to 86), given by Wilson and Meyer (1969), but the tail length-total length ratio (0.326) is greater than that previously reported for male *A. veliferum* (0.277 to 0.319). The anterior temporal is fused with the upper temporal in the second row on the left side (1+2, the normal condition, on the right), a condition seen in only one other specimen (from Panamá). As is the case for specimens of *A. veliferum* from Nicaragua to Panamá, there is no loreal. Infralabials number 9-9, and other cephalic scutellational features are typical for the species.

One would certainly not recognize a subspecies in a known variable species on the basis of a single specimen. The second specimen, besides establishing the presence of a linking Atlantic-Pacific population, possesses enough "typical" characteristics to invalidate any suspicion that Pacific versant individuals might represent a taxonomically recognizable subgroup. In MNCR 3142 there are 130 ventrals, the tail is incomplete, and other scutellational features are typical, except that there are a number of atypical additions and deletions of scale rows along the length of the animal.

Coloration of both specimens is similar to that of others from Costa Rica, and shows no approach to the lighter Panamanian specimens (Wilson and Meyer, 1969). The right hemipenis is everted on MNCR 2819, and closely resembles that of a specimen from Honduras, described and pictured by Wilson and Meyer.

That MNCR 2819 should show so many external morphological peculiarities is, at first analysis, striking. The species *Amastridium veliferum*, compared to most other colubrid snakes, is unusual, however, in the type of variation in several morphological features, such that the first four specimens collected were described as different genera and species. Since 1925, *Amastridium* has been considered to consist of two species, synonymized by Wilson and Meyer (1969). As Scott (1967) stated, "as intraspecific variation becomes better known, the fallacy of the constancy of 'key' characters at the specific or generic level in colubrid snakes becomes increasingly apparent."

While examining MNCR 3142 for stomach contents, the junior author noted certain peculiar-

ities in the reproductive system of what, on the basis of external examination, appeared to be a male specimen. This specimen has one everted hemipenis, however, the internal reproductive system is that of a female. Although somewhat damaged during dissection, the specimen has a pair of swollen, convoluted oviducts and what appear to be elongate ovaries, which are in the correct relative positions for snakes (right ovary anterior to the left). Comparison of the hemipenis of this specimen with that of an unequivocal male (testes and vasa deferentia present) from Honduras (LACM 45150) demonstrates that the hemipenis of MNCR 3142 is aberrant. It is relatively small and thin, spines are absent the length of the organ, the sulcus spermaticus is shallow and poorly formed, and there are some atypical conical lobes on the absulcate surface. A *m. retractor penis magnus* is present.

This pseudohermaphroditic specimen was probably a functional female, but the presence of hemipenes and associated muscles would cause one to consider this animal a male when using the conventional means of sex determination and this might account for the preponderance of apparent males from the southern portion of the range, which was noted by Wilson and Meyer (1969). Only internal dissection of the specimens from this portion of the range can resolve this question. At any rate, MNCR 2819, a specimen from this area, is a typical male.

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NEWS AND NOTES

NEW FORMAT

With this issue, the Southern California Academy of

Sciences begins a new era of publications. The

Bulletin has been redesigned and will appear three

times yearly. Hopefully, the Bulletin will now serve

its community better by providing more information

to all members. During the period of transition,

from the old single column to the new format, more

time than anticipated was required. The three

numbers of the Bulletin will be issued on April 30,

August 31, and December 31.

350 Golden Shore, Long Beach, accepted a new industrial position with Southern California Edison. Ron will be investigating the environmental impact of thermal discharges, antifouling equipment, and impregnation studies to prevent fouling. Ron is a fulltime employee of Southern California Edison as biologist-diver.

OIL POLLUTION REPORT

Copies of the two volume University of Southern California

Oil Pollution Report are now available.

Copies may be purchased through Mrs. Dorothy

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COVER ILLUSTRATION

An illustration will appear on the front of every issue of

the Bulletin. The first number of each volume will

always have a color frontispiece. The cover illustration

will not necessarily be from or related to one

of the contributions, although it is required to be

related to our area. Authors and members of the

Academy may submit to the Editor copies of artwork

which they believe appropriate for the Bulletin

cover.

NEWS SECTION

A new section has been created to print relevant news

relating to the southern California community.

News of any nature or field of endeavor will be

acceptable. The News and Notes section will also

consider reviews, comments, and any type of

announcement. This section will stress current news

as well as that of particular interest to our area.

Submit copy for publication to the office of the

Managing Editor.

INDUSTRY AND ENVIRONMENT

On April 19, 1971 Alec R. Strachan, formerly with

the California Department of Fish and Game,

RARE AND ENDANGERED WILDLIFE

On May 21, 1971, the Fish and Game Commission of

the state of California declared that any species of

wildlife considered to be rare or endangered would

be prohibited to collect. The list of rare and en-

dangered fish and wildlife adopted by the California

Fish and Game Commission is available from B. E.

Faist, Wildlife Protection Branch, Department of

Fish and Game, 1416 Ninth Street, Sacramento,

95814.

LLOYD W. BARKER
APRIL 25, 1949

In the early morning hours of Tuesday, June 29, 1971, a vessel

under tow by the Coast Guard went down in rough seas between Santa Rosa and Santa Cruz Islands. Besides the numerous sea lions in cages, three individuals were aboard this ill-fated craft. This accident proved fatal to one young man and all the sea lions.

The career of Lloyd W. Barker ended in the dark, cold waters of the Santa Barbara Channel. Lloyd was acting as an official observer on a commercial vessel catching California sea lions. He was representing the California Department of Fish and

Game, which had been under pressure by the Sierra Club to have an observer on each such commercial vessel. It seems that the issuance of a permit, and its implied regulations, were insufficient for the Sierra Club.

Lloyd was a student at Humboldt State College and spent his summers working for the California Department of Fish and Game. He had an intense interest in the California fossil fish record as well as the recent fauna. Lloyd's cheerful outlook on life and warm personality will be missed for it had special significance to those of us fortunate to know him.

SOME FORTHCOMING CONTRIBUTIONS

New species of *Polydora* (Polychaeta: Spionidae) from the coast of California. By *James A. Blake* and *Keith H. Woodward*

The microhabitats of western wolf spiders of the genus *Pardosa*. By *Donald C. Lowrie*

Two types of aggregation grouping in the large milkweed bug, *Oncopeltus fasciatus* (Dallas) (Hemiptera, Lygaeidae). By *Steven R. Kutcher*

The larvae of *Pagurus samuelis* (Stimpson) (Decapoda, Anomura) reared in the laboratory. By *Floy E. MacMillan*

A new species of *Iphitima* (Polychaeta) from *Cancer antennarius* (Crustacea: Decapoda). By *John Pilger*

INSTRUCTIONS FOR AUTHORS

Contributions to the BULLETIN may be in any of the fields of science, by any member of the Academy. Acceptance of papers will be determined by the amount and character of new information and the form in which it is presented. Articles must not duplicate in any substantial way, material that is published elsewhere. Manuscripts that do not conform to BULLETIN style will be returned to the author. All manuscripts will be handled through an editorial board working in cooperation with the Editor.

Manuscript Form—(1) The 1964 AIBS Style Manual for Biological Journals is recommended as a guide, but where there is a conflict, the BULLETIN style will prevail. (2) Type write material, using double spacing throughout, including Literature Cited, and leaving a minimum of one inch margins, on only one side of 8½ x 11 inch standard weight paper. (3) Submit two copies. (4) Place tables on a separate sheet of paper. (5) Footnotes should be avoided if possible. (6) Legends for figures and unavoidable footnotes should be typed on separate paper. (7) Method of literature citation *must* conform to BULLETIN style—see Volume 70 and later issues. Spell out in full the titles of non-English serials and places of publication. (8) All manuscripts, except research notes, must be provided with an abstract at the beginning of the article. (9) Acknowledgments should be placed just before literature cited. (10) Short reports may be submitted as research notes—see Volume 70 and later issues for style.

Illustrations—All illustrations, including maps and photography, must be referred to as "Figures." Illustrations *must* not be larger than 8½ x 11 inches; they may be either the original or glossy print. All illustrations must be in proper proportions for reduction to BULLETIN page size. Submit one photoduplicated copy of each illustration with the manuscript.

Cover photograph—A photograph will be printed on the cover of each issue. This may either be a photograph used in one of the articles or a photograph of something of scientific interest to southern California. Consult the Editor for selection of such material.

Proof—Author will be sent proof which should be corrected and returned promptly to the Managing Editor. Changes, other than typesetting errors, will be billed to the author. Orders for reprints should be sent to the Managing Editor at the time corrected proof is returned; appropriate order forms will be included when proof is sent. The BULLETIN does not furnish free reprints.

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COVER: *Algal community at Eel Point, San Clemente Island, one of the offshore channel islands of southern California. The dominant algal forms include the surf grass, *Phyllospadix*, in the immediate foreground and background; sargassum weed, *Sargassum agardhianum*, hanging down from the top of the exposed rock; *Halidrys dioica*, along the face of the exposed rock with black abalones; and a patch of algal turf is exposed at the base of the exposed rock at the righthand margin.*

Photograph by Donald B. Bright

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BULLETIN OF THE SOUTHERN CALIFORNIA
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THE LARVAE OF *PAGURUS SAMUELIS* (DECAPODA: ANOMURA)
REARED IN THE LABORATORY

FLOY E. MACMILLAN¹

ABSTRACT: *Pagurus samuelis* (Stimpson) larvae from northern California were studied. Larvae were raised at 15 and 17°C. Illustrations and descriptions of the four zoeal stages and glaucothöe are presented. The zoea are compared with descriptions of zoea of this species from Japan.

Over 100 species of the genus *Pagurus* have been described. Few of these (Provenzano and Rice, 1964) have had their larval stages described and many descriptions have been so general that it is impossible to distinguish planktonic larvae of different species.

Four species of *Pagurus* are commonly found in the intertidal regions of the northern California coast: *P. granosimanus* (Stimpson), *P. hemphilli* (Benedict), *P. hirsutiuculus* (Dana), and *P. samuelis* (Stimpson). Larval stages of the first three species have been described by Mr. William Hall and will be published later. Coffin (1960) described the ovulation, embryology and developmental stages of *P. samuelis*; however, his description of the larval stages was of a general nature. Kurata (1968) also briefly described the larvae of this species from Japan, but his larvae differ significantly from California material.

Provenzano and Rice (1964), Greenwood (1966), Scelzo and Boschi (1969) and Roberts (1970) have described larvae of *Pagurus* species comparing the setation and appendages of each larval stage as well as the overall size and appearance of the zoea and glaucothöe. My purpose is to redescribe the larval stages of *Pagurus samuelis* in a similar manner so that details will be available to help identify planktonic forms. Differences observed between California *P. samuelis* and the accounts of the species from Japan are compared.

I wish to extend my thanks to the Pacific Marine Station for use of their facilities and to Mr. William Hall and Dr. James A. Blake for critically reviewing this manuscript. This summer study was supported by National Science Foundation Grant (GB-19344).

METHODS

Seven ovigerous females were collected on July 28, 1970 at Estero de San Antonio, two miles north of Dillon Beach, California. The specimens were found living in shells of *Tegula funebris* (A.

Adams) and *Tegula brunnea* (Philippi) in a protected rocky intertidal area. In the laboratory each female was kept in a plastic aquarium containing sea water. On July 29, 1970, one of the females yielded over 250 larvae.

The larvae were separated and placed in culture dishes. One hundred and eight larvae were placed in 5.5 mm bowls, 3 per bowl, with approximately 25 ml of filtered sea water. One hundred sixty-eight larvae were placed in 10 mm bowls, 7 per bowl, with 200 ml of sea water. After the first molt, and a number of fatalities, all the larvae were maintained in the larger bowls with only 3 per 200 ml of water. Freshly hatched *Artemia* nauplii were added as food. The bowls were placed in refrigerators in which the temperatures were kept constant at 15 and 17°C. Salinity varied from 30‰ to 35‰. Water was changed every other day and fresh *Artemia* nauplii were added daily.

Ten to 20 specimens of each instar and the exuviae were preserved in ethylene glycol. Drawings of the whole larvae were made from specimens narcotized with propylene phenoxytol (0.15%) and from preserved specimens. At least 5 specimens of each instar were dissected and studied in detail with respect to setation, segmentation, size and form. Drawings of dissected appendages were checked against the exuviae.

Duration of each stage represents time spent in a given instar by larvae which successfully molted to the next instar.

Measurements were made using an ocular micrometer. Total length (TL) represents a measurement from the tip of the rostrum to the posterior border of the telson exclusive of the telson processes. Carapace length (CL) represents a measurement taken from the tip of the rostrum to the tip of the posterolateral carapace spines. All measurements are accurate to within ± 0.1 mm.

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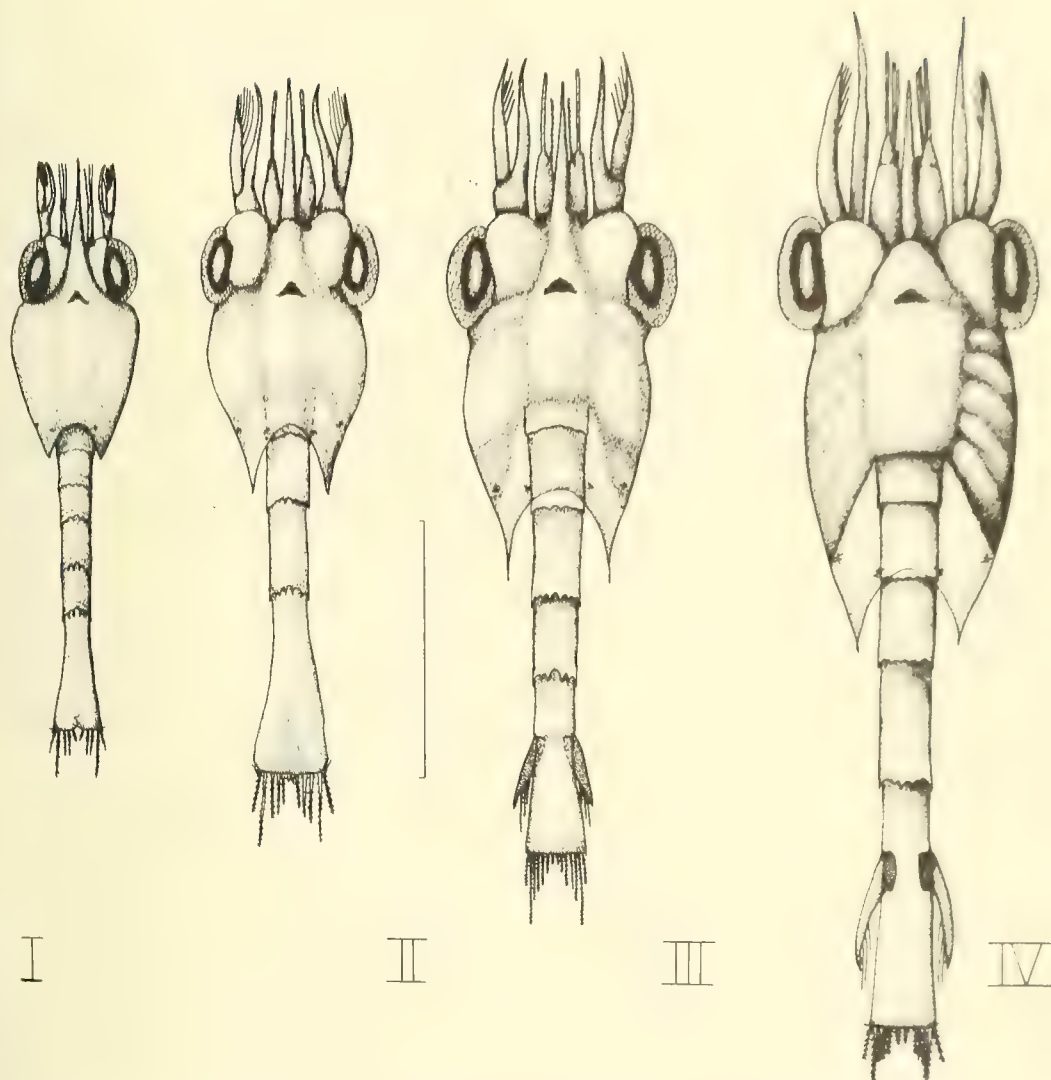


Figure 1. *Pagurus samuelis* (Stimpson). Dorsal views of zoeal stages I-IV. Scale 0.5 mm.

FIRST ZOEAL (Figure 1 I, 2 I)

Size: CL, 1.1 mm; TL 2.4 mm

Duration: 6-7 days at 15 and 17°C

General Characteristics

The eyes are sessile. The rostrum is long, extending almost to the tip of the antennal endopodite. The carapace bears 2 short downward projecting hooks on the posterolateral margins. The abdomen is composed of 5 distinct somites and a sixth which is fused with the telson. Somite 1 lacks spines; somites 2-5 each bear 2 pairs of short postero-dorsal spines which increase in size from somite 2-5. In addition, somites 2-4 have another pair of smaller dorsolateral spines. There is a pair of short

lateral spines on somites 2-5. The telson (Fig. 3 I) is longer than wide, with the longest setae as long as the telson itself. The posterior margin is straight with a distinct, almost v-shaped, notch. There are 7 telson processes on each side; the outermost is a heavy spine, the second a delicate hair, the others are articulated plumose setae.

Coloration

The dorsal surface just posterior to the eyes contains a prominent yellow chromatophore. The eyes also contain a yellow pigment giving them an iridescent appearance. The base of each mandible contains a deep red chromatophore. There are red chromatophores posterior to each antennule and 8

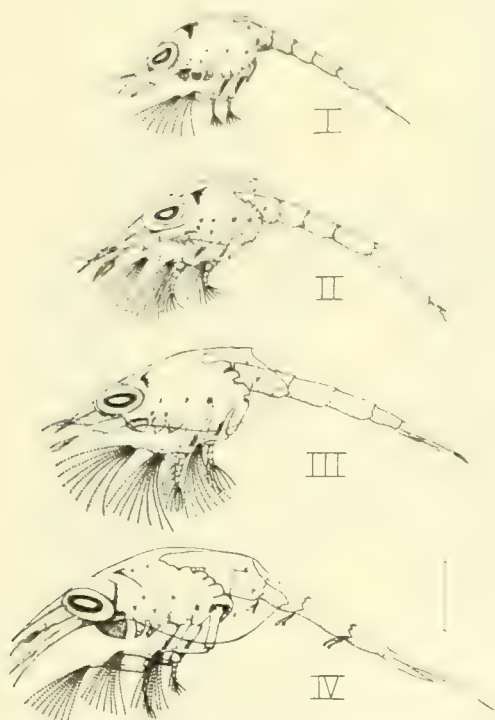


Figure 2. *Pagurus samuelis* (Stimpson). Lateral views of zoeal stages I-IV. Scale 0.5 mm.

small red-pigmented cells over the lateral surfaces of the carapace. The basipodite of maxillipeds 1-2 bears a prominent red chromatophore.

Appendages

Antennule (Fig. 4 I) is uniramous and terminally bears 2 aesthetes and 2 fine hairs. Subterminally there is a long plumose seta.

Antenna (Fig. 4 I) is biramous. The endopodite is fused to the basipodite. It lacks terminal setae and reaches almost to the tip of the antennal scale spine. There is a ventral untoothed spine on the endopodite near the base of the antennal scale. The antennal scale is 8 times as long as it is wide. It bears a long tooth terminally and 4 long plumose setae and 1 shorter plumose seta along the medial margin.

Mandibles (Fig. 5 I) are asymmetrical. Each has an incisor, a molar process, and a number of corneous teeth.

Coxal endite of the maxillule (Fig. 5 I) bears 4 plumose setae and 1 nonplumose seta terminally. The basal endite has 2 very stout teeth and 2 smaller spines, with each tooth bearing a number of spinules. Endopodite bears 3 nonplumose setae on the distal segment and an additional nonplumose seta on the middle segment.

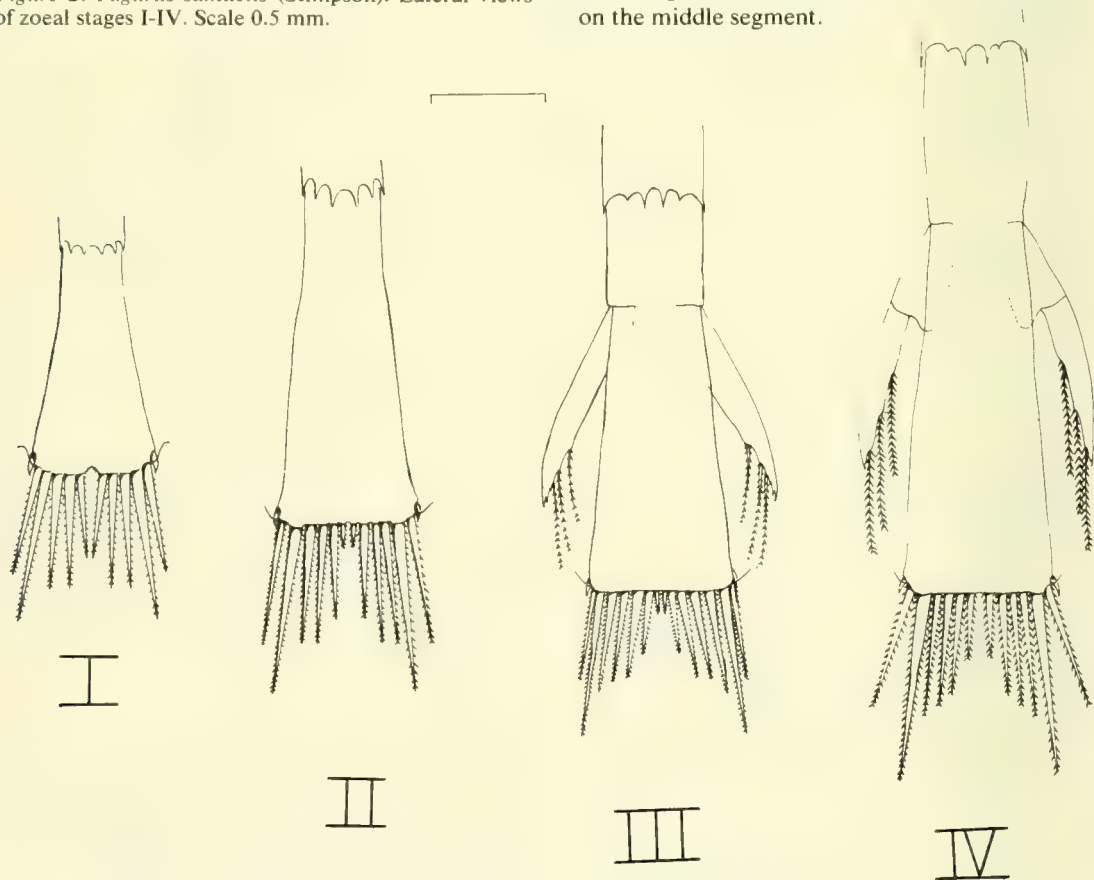


Figure 3. *Pagurus samuelis* (Stimpson). Telson of zoeal stages I-IV. Scale 0.2 mm.

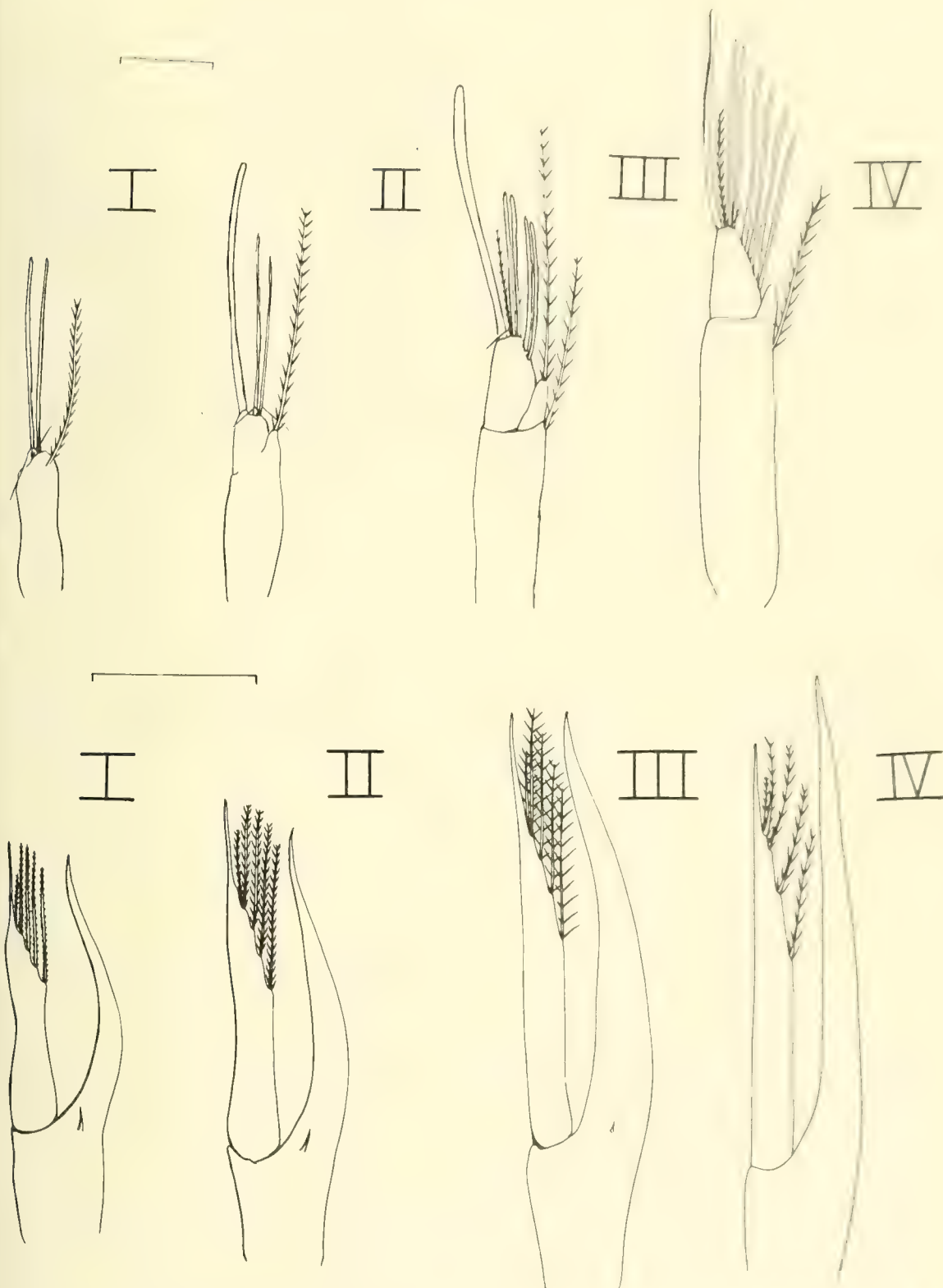


Figure 4. *Pagurus samuelis* (Stimpson). Top, antennules of zoeal stages I-IV. Scale 0.1 mm. Bottom, antennae of zoeal stages I-IV. Scale 0.2 mm.

Scaphognathite of the maxilla (Fig. 5 I) has 5 plumose setae along the margin. The endopodite bears 3 plumose setae terminally and 2 setae subterminally on the medial margin. The distal and proximal lobes of the basal endite each have 1 subterminal and 3 terminal plumose setae. The distal lobe of the coxal endite has 2 terminal setae and 1 subterminal seta. The proximal lobe has 4 terminal setae.

Basipodite of the maxilliped 1 (Fig. 6 I) has a pair of plumose setae at the anteromedial corner and 6-7 hairs on the medial margin. The exopodite is composed of 2 indistinct segments and terminates in 4 long plumose setae. Endopodite is five-segmented, the terminal segment bearing 4 terminal plumose setae and a fifth on the lateral margin. The penultimate segment has a heavy plumose seta and a finer plumose seta on the distal medial margin. The antipenultimate segment bears a single heavy seta on the distal medial margin and a row of fine setules on the lateral margin. The next proximal segment bears a heavy plumose seta and a nonplumose seta on the distal medial margin, and a fine row of setules on the lateral margin. The proximal segment has 3 nonplumose setae on the distal medial margin and, again, a row of setules on the lateral margin.

Basipodite of the maxilliped 2 (Fig. 7 I) has 1 seta on the anteromedial corner and 2-3 hairs along the medial margin. The exopodite consists of 2 indistinct segments and bears 4 terminal plumose setae. The endopodite has 4 segments; the terminal segment bearing 4 terminal plumose setae and 1 subterminally. The other segments each have 1 heavy plumose seta and 1 fine plumose seta on the distal margin. In addition, the antipenultimate segment has a row of fine setules on the lateral margin.

Maxilliped 3 (Fig. 8 I) is a uniramous rudiment.

SECOND ZOEAL (Figure 1 II, 2 II)

Size: CL 1.4 mm; TL 2.6 mm

Duration: 6-8 days at 15 and 17°C

General Characteristics and Coloration

The eyes are mobile and limb buds are visible under the carapace behind maxilliped 3. The telson (Fig. 3 II) remains fused with abdominal somite 6 but the median notch has disappeared, and there is an additional pair of short medial telson spines.

The coloration is essentially the same as in the previous stage except that the red chromatophores are more distinct. The pigmented cells on the carapace are now clearly red chromatophores.

Appendages

Antennules (Fig. 4 II) terminate in 1 long aesthete, 2 shorter aesthetes and 2 small hairs.

Antennae (Fig. 4 II) have elongated but are identical to that of zoeal stage I in form and setation. There is an extremely small tooth at the base of each antennal scale.

Mandibles (Fig. 5 II) are similar in shape to those of the previous stage, but there is an increase in the number of corneous teeth.

Maxillules (Fig. 5 II) differ from those of the first zoeal stage with the addition of 2 heavy spicule-bearing spines on the basal endite. There is also an additional small spine proximally on the basal endite and an additional small terminal spine on the coxal endite.

Scaphognathite of the maxilla (Fig. 5 II) bears an additional seta on the lateral margin. The setation and form of the basal and coxal endites remain unchanged.

Basipodite of the first maxilliped (Fig. 6 II) has 2 fine setae and a short hair at the distal medial corner. There are 4 setae and 1-2 additional fine hairs on the medial margin. The exopodite terminates in 7 natatory setae. The setation of the terminal and penultimate segments remains unchanged but the antipenultimate and the 2 proximal segments each bear a long plumose seta on the lateral margin in place of the setule rows present in zoeal stage I.

Basipodite of maxilliped 2 (Fig. 7 II) bears 2 setae on the distal medial corner and 1-2 setae along the medial margin. The exopodite terminates in 7 natatory setae. The setation of the endopodite remains unchanged except that a long plumose seta has replaced the row of setules on the second proximal segment.

Maxilliped 3 (Fig. 8 II) consists of a basipodite and an exopodite with 6 natatory setae.

THIRD ZOEAL (Figure 1 III, 2 III)

Size: CL 1.5 mm; TL 2.6 mm

Duration: 7 days at 17°C

General Characteristics and Coloration

Abdominal somite 6 is incompletely fused to the telson. There is no dorsal spine on this somite. The telson (Fig. 3 III) is twice as long as it is wide; the number and relative length of the telson spines is unchanged. Uropods consisting of a fused protopodite and exopodite are present. The exopodite bears 3 small teeth and 3 plumose setae on the medial margin. Coloration is unchanged.

Appendages

Antennules (Fig. 4 III) are segmented and biramous. The distal segment terminally bears 1 large and 2 small aesthetes, 1 plumose seta and 2 hairs. Subterminally, there is an additional pair of aesthetes. The segment representing the ventral

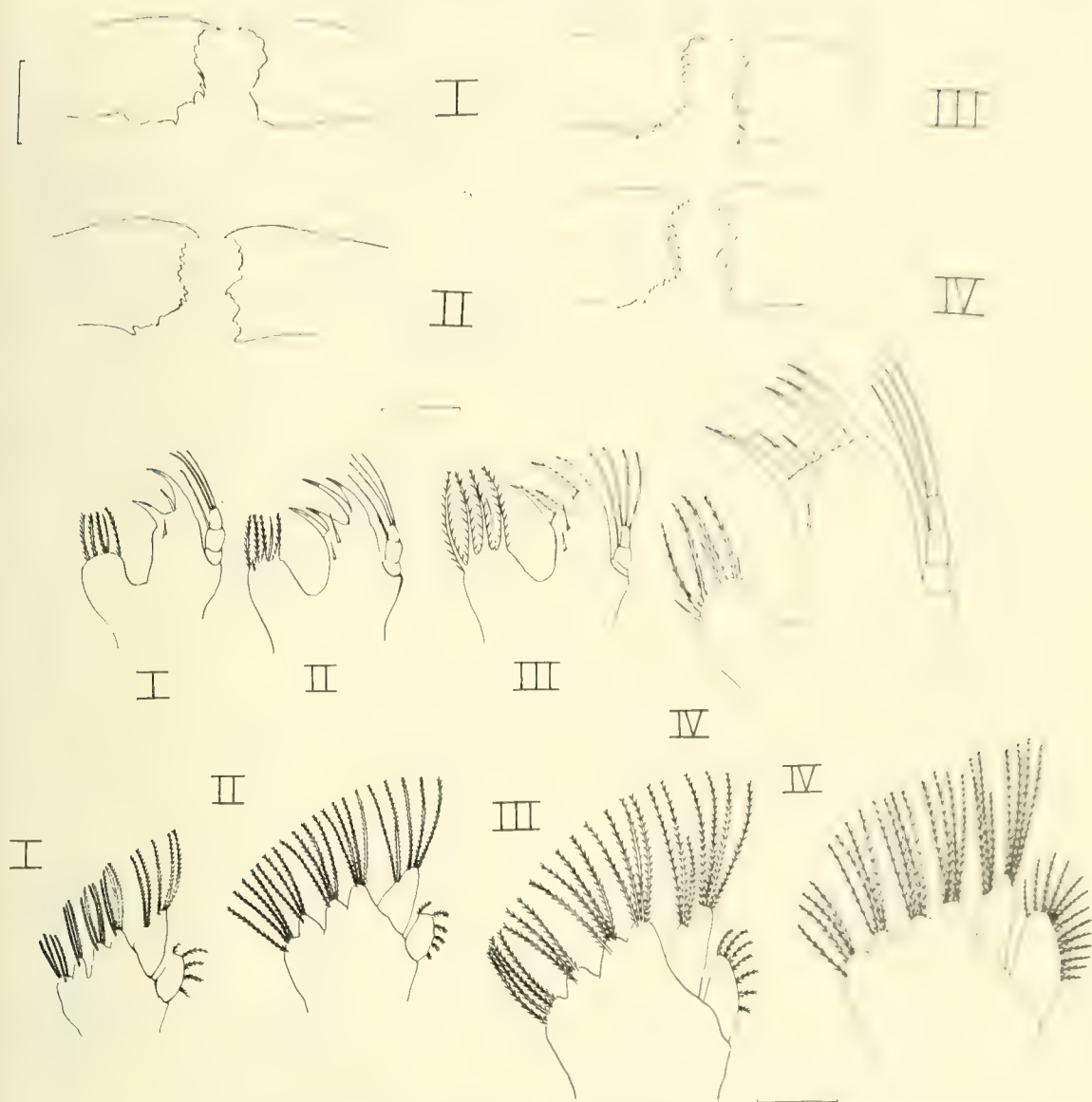


Figure 5. *Pagurus samuelis* (Stimpson). Top, mandibles of zoeal stages I-IV. Center, maxillules of zoeal stages I-IV. Bottom, maxillae of zoeal stages I-IV. Scales 0.1 mm.

flagellum bears a single long plumose seta. The peduncle has a long plumose seta on the distal margin.

Antennal scale (Fig. 4 III), excluding the terminal tooth, is 8 times as long as wide. On some specimens the terminal tooth was shortened, and in a few cases was forked at the tip. The ventral tooth on the endopodite is reduced and the margin beneath the antennal scale is untoothed.

Mandibles and maxillules (Fig. 5 III) are unchanged.

Scaphognathite of the maxilla (Fig. 5 III) bears

7 plumose setae along the margin. The endopodite bears 4 terminal and 3 subterminal plumose setae. The setation of the basal and coxal endites is unchanged.

Exopodite of maxilliped 1 (Fig. 6 III) bears 7 natatory setae; the endopodite and basipodite are unchanged.

Maxilliped 2 (Fig. 7 III) is unchanged except that the exopodite has 8 natatory setae.

Maxilliped 3 (Fig. 8 III) has an endopodite terminating in 1 small plumose seta. The exopodite has 7 natatory setae.

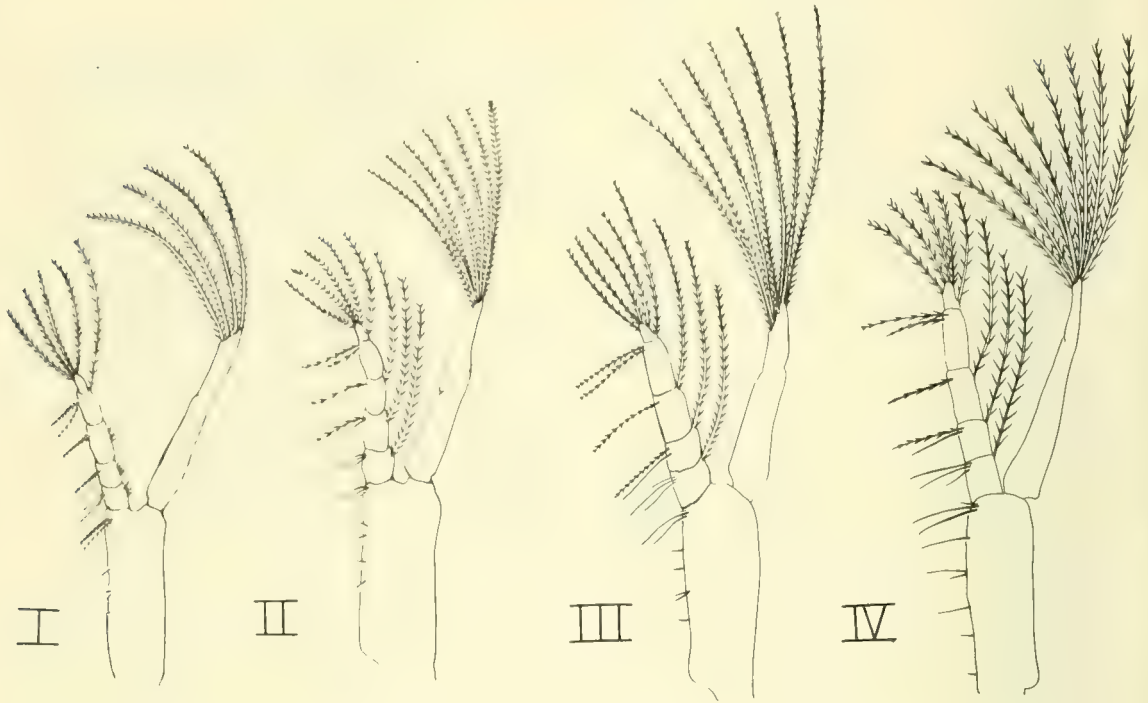


Figure 6. *Pagurus samuelis* (Stimpson). First maxillipeds of zoal stages I-IV. Scale 0.5 mm.

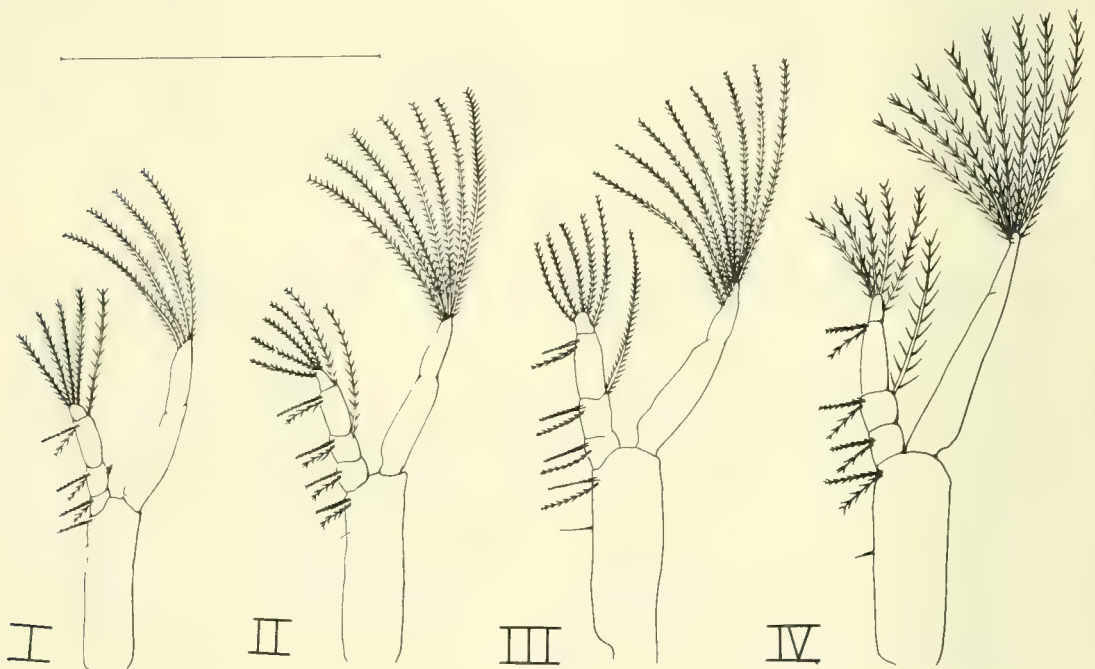


Figure 7. *Pagurus samuelis* (Stimpson). Second maxillipeds of zoal stages I-IV. Scale 0.5 mm.

FOURTH ZOEAL STAGE (Figure 1 IV, 2 IV)

Size: CL 2.2 mm; TL 3.4 mm

Duration: 7-8 days at 17°C

General Characteristics and Coloration

Pleopod buds are present on abdominal somites 2-5. Telson (Fig. 3 IV) is almost 3 times as long as wide. Protopodites of the uropods are articulated with the exopodites but not with the endopodites. There is an additional yellow chromatophore on the rudimentary cheliped and a red chromatophore just above the basipodite of maxilliped 3.

Appendages

The process representing the dorsal flagellum of the antennule (Fig. 4 IV) bears 3 aesthetes, 1 plumose seta, and 2 hairs. In addition, there is a longitudinal row of 4-5 subterminal aesthetes. The ventral flagellum has lost its terminal seta but has retained the plumose seta at its base.

The endopodite of the antenna (Fig. 4 IV) is slightly wider than the antennal scale and extends beyond the tip of the antennal scale spine.

Mandibles (Fig. 5 IV) are unchanged. No palp is present.

Coxal endite of the maxillule (Fig. 5 IV) bears 2 additional nonplumose setae. The basal endite bears 6 heavy spines, each with secondary spinules. The endopodite is unchanged.

Scaphognathite of the maxilla (Fig. 5 IV) bears 13 plumose setae. Setation of the endopodite and of the basal and coxal endites is unchanged.

Exopodite of maxilliped 1 (Fig. 6 IV) bears 8 natatory setae; the endopodite and basipodite are unchanged.

Maxilliped 2 (Fig. 7 IV) is unchanged.

Exopodite of maxilliped 3 (Fig. 8 IV) bears 8 natatory setae. The endopodite bears 1 terminal plumose seta and 1 subterminally.

GLAUCOTHÖE (Figure 9, 10)

Size: CL 1.4 mm; TL 3.4 mm

General Characteristics and Coloration

Periopods are functional. The 4 pairs of pleopods are well developed and used in locomotion. The rostrum is blunt. The telson (Fig. 10 a) is only slightly longer than its width and has only 8 terminal plumose setae. There are 5 pairs of small setae on the dorsal surface and 1 pair on the lateral margin. The protopodites of the uropods are articulated with both the endopodites and exopodites. The endopodites bear a single terminal seta. The exopodites are subequal, the left being slightly larger than the right. Each has 10 long plumose setae along the margin. In addition, there are 5-7 corneous granules and 4-5 smaller setae along the margin.



Figure 8. *Pagurus samuelis* (Stimpson). Third maxillipeds of zoeal stages I-IV. Scale 0.5 mm

Red chromatophores are prominent on the eyestalks, antennules, antennal basipodites, and on the anterolateral region of the carapace. There are a great number of pale yellow chromatophores scattered over the anterior dorsal region of the carapace, the eyestalks, and the fifth pereopod.

Appendages

The ventral flagellum of the antennule (Fig. 10 R) consists of 2 segments. The terminal segment bears 8 small setae; the proximal segment bears 2-3. The dorsal flagellum consists of 4 segments. The most proximal is unarmed. The other segments each have 3-4 aesthetes. In addition, the terminal and the next most proximal segments bear several fine setae.

Antenna (Fig. 10 Q) has a scale at its base which terminates in 2 nonplumose setae. There are 10 flagellary segments, each of which bears a few short setae.

Mandibles (Fig. 10 P) are cuplike and have a two segmented palp which terminates with four small hooks.

Endopodite of the maxillule (Fig. 10 O) has lost its segmentation and has 1 seta. The basal endite bears 12 spines distally and 2 proximally. The coxal endite bears 10-14 setae.

Maxilla (Fig. 10 N) bears 27 setae on the margin of the scaphognathite which has increased in proportion to the rest of the maxilla. The scaphognathite and endopodite are no longer articulated with the endites.

Maxilliped 1 (Fig. 10 M) is radically changed. The basipodite is broad and appears bilobed. It has 15 setae on the distal lobe and 4 setae on the proximal lobe. The endopodite and exopodite are reduced and have only 3-4 short terminal setae.

Exopodite of maxilliped 2 (Fig. 10 L) bears 5 long plumose setae. The endopodite consists of 4 segments, each with a few short setae.

Exopodite of maxilliped 3 (Fig. 10 K) has 6

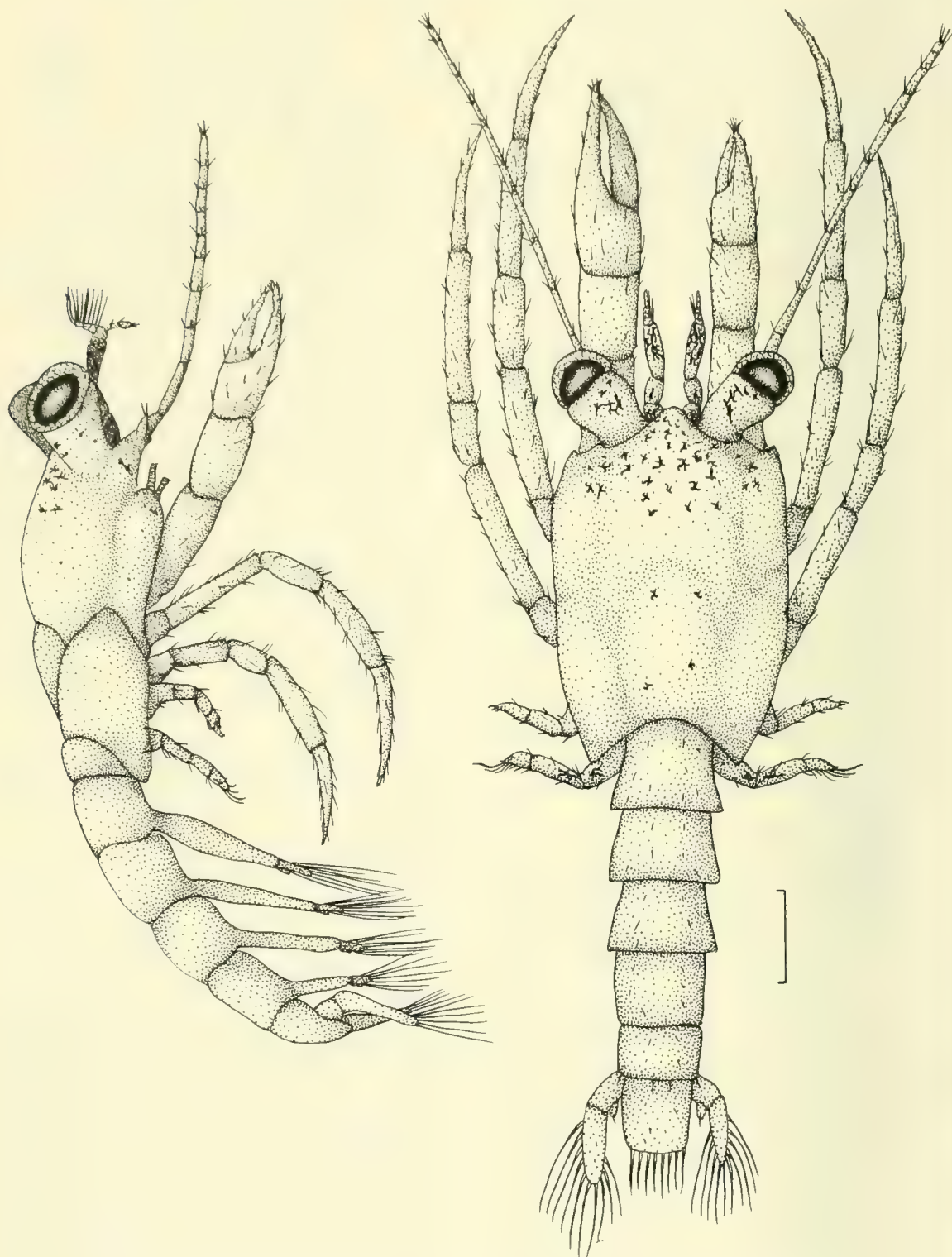


Figure 9. *Pagurus samuelis* (Stimpson). Glaucothöe. Lateral and dorsal views. Scale 1.0 mm.

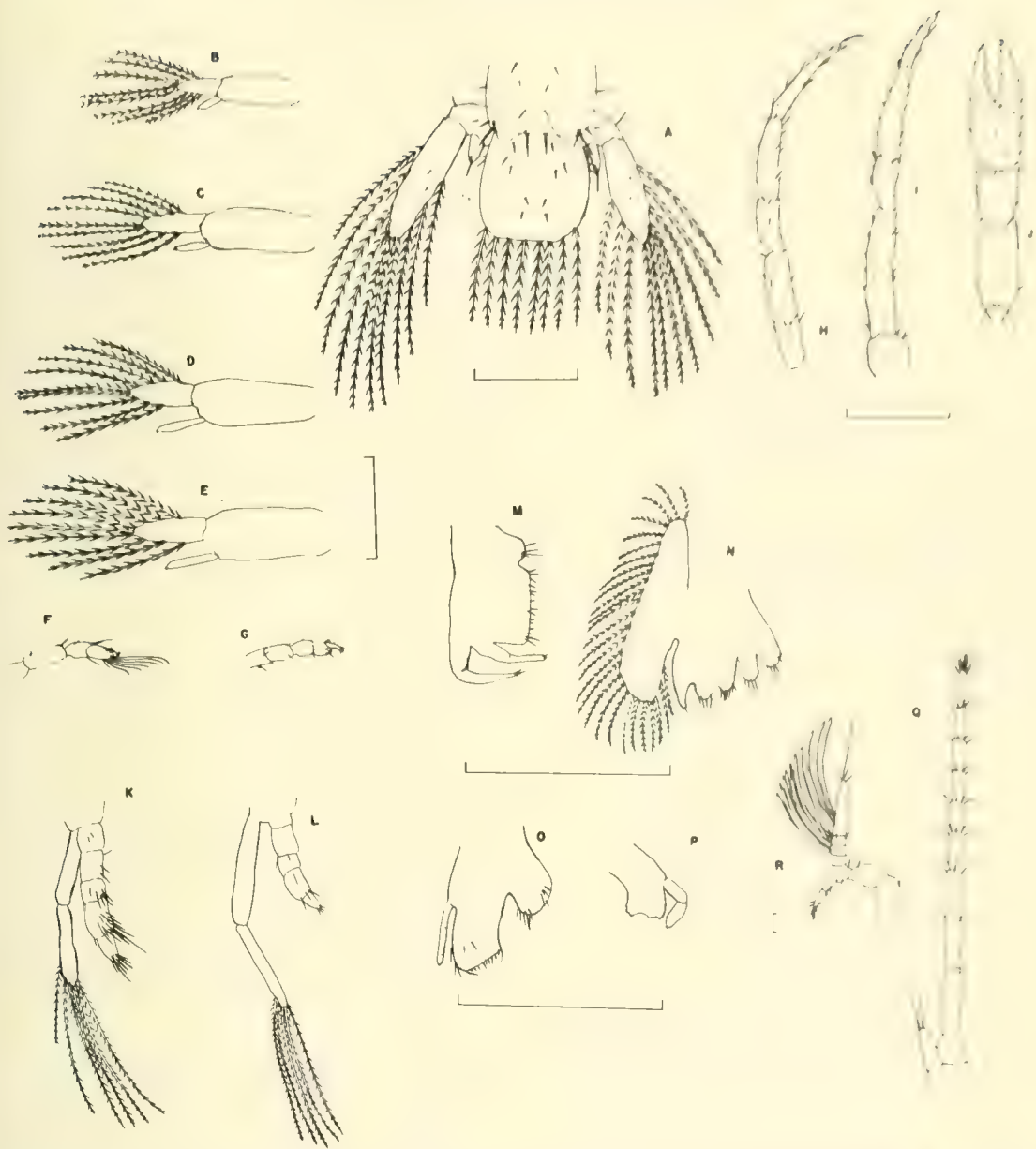


Figure 10. *Pagurus samuelis* (Stimpson). Glaucothöe. A, telson; B-E, pleopods; F, fifth periopod; G, fourth periopod; H, third periopod; I, second periopod; J, cheliped; K, third maxilliped; L, second maxilliped; M, first maxilliped; N, maxilla; O, maxillule; P, mandible; Q, antenna; R, antennule. Scale 0.5 mm.

plumose setae. The endopodite has 5 segments. The ultimate and penultimate segments are heavily armed with setae, many of which have setules.

The chelipeds (Fig. 10 J) are subequal in size; the left being larger than the right. Periopods 2 and 3 (Fig. 10 H-I) have dactyli as long as the propodi. Periopod 4 (Fig. 10 G) is nonchelate. The propodus has 4 corneous granules on the ventrolateral surface. Periopod 5 (Fig. 10 F) has 7 granules and 7 long setae on the propodus.

Pleopods (Fig. 10 B-C) are biramous. Endopodite of each bears 2 small hooks. Exopodites of the pleopods on somites 2-4 bear 9 plumose setae, whereas the pleopod of somite 5 has only 8.

DISCUSSION

The purpose of the present study is to extend an earlier work on *Pagurus samuelis* larval development by Coffin (1960). Coffin did not make a detailed study of the larval appendages, making

TABLE 1. Morphological differences between Japanese and California zoea larvae of *Pagurus samuelis*.

Characteristic	Japanese Species	California Species
Rostral length	extends to base of antennal scale spine	extends beyond tip of antennal scale spine
Antenna endopodite scale	forked	not forked
	broad, concave outer margin with six plumose setae	narrow, straight outer margin with five plumose setae
tooth at base	articulated	not articulated
Fifth abdominal segment	prominent lateral spines	short lateral spines
Telson	wide — convex outer margin	narrow — straight outer margin
Coloration chromatophores on carapace	all on ventral margin	scattered on lateral surface
chromatophores at base of rostrum and on antennal protopods	present	absent

differentiation of planktonic larvae difficult if species other than *P. samuelis* are encountered. He mentioned briefly the presence of setae on the antennule and antennal scale, the number of setae on the exopods of the maxillipeds, and the setae on the uropods and telson, but did not describe the mandibles, maxillules, and maxillae. Coffin did not state the number of setae on the antennal scale spine, but his drawings suggest only 4. In the present study 5 were found. The spine Coffin described on the end of the uropod in the third zoea is composed of 3 small spines.

Pagurus samuelis larvae described by Kurata (1968) differ from the California larvae in 5 aspects outlined in Table I. Differences in the telson shape, antennal structure and lateral abdominal spines are highly significant and it is probable that the California and Japanese *P. samuelis* are actually separate species.

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DESCRIPTIONS AND NOTES CONCERNING SOME ORIENTAL *APHILOCHEIRUS*
(HEMIPTERA: APHELOCHEIRIDAE)

IRA LA RIVERS¹

ABSTRACT: Two new species of *Aphelocheirus* are described from India and *A. pallens* Horvath is noted from additional localities in New Guinea.

During an investigation of the Naucoridae and Aphelocheiridae of New Guinea, specimens were examined from surrounding areas in an attempt to understand the relationships and origins of the very unique fauna which exists in New Guinea. This work turned up additional records of *Aphelocheirus pallens* Horvath 1899 in New Guinea as well as two new species of *Aphelocheirus* from a related fauna in the southeastern Asiatic mainland.

Aphelocheirus pallens Horvath

In 1899, Horvath described this species from German New Guinea, in the northeast section of the island. In my perusal of the literature, I have not seen it recorded elsewhere, but in the Leiden and Bishop museums' collections, there are additional specimens from the western part of New Guinea, as follows: Neth. Ind.-American New Guinea Exped., Araucaria Camp, 800 m, 1939 Mar. 3, L. J. Toxopeus; Same, Mist Camp, 1800 m, (Leiden Museum localities); New Guinea, Neth., Bodem, 10 m, 11 km SE of Oerber-faren, 1959 July 7-17, T. C. Maa, and New Guinea, NW, Nabire, S. Geelvink Bay, 10-40 m, 1962 Oct. 13, N. Wilson (Bishop Museum localities).

***Aphelocheirus pygmaeus*, new species**

Figure 1

General: The smallest species that I have seen in the genus, measuring 4 by 2 mm, approaching the genus *Potamocoris* of the family Naucoridae in size and gross appearance. Darker in color anteriorly with some yellow bordering, hemelytra lighter. Venter blackish-brown with some yellow lightening anteriorly, legs yellowish.

Head: Blackish brown, shiny with sparse pitting. Anteclypeus greatly expanded and protuberant before eyes, its anterior outline reasonably smoothly circular. Eyes blackish, essentially flush with surface; hyperocheal angle not discernible as such. Labrum large, prominent. Head ratios are: (1) Total length-to-width (including eyes) 25: 34 (74%), (excluding eyes and utilizing widest interocular

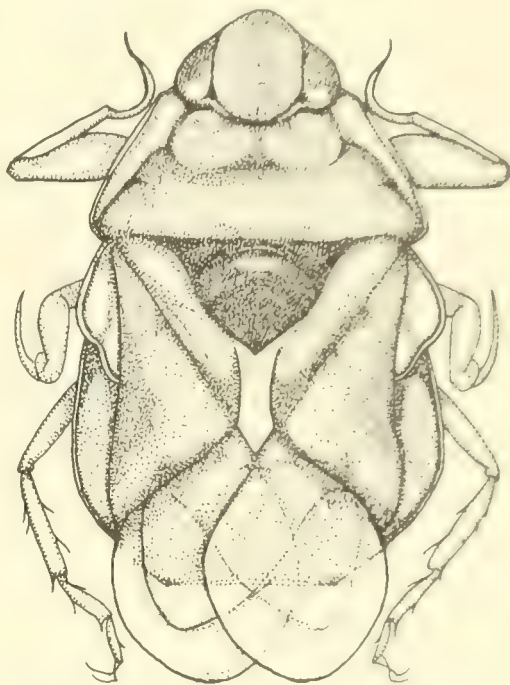


Figure 1. *Aphelocheirus pygmaeus*, new species, holotype female.

space) 25: 21 (84%); and (2) anterior distance between eyes to posterior distance between eyes 21: 21 (inner margins are not parallel, but curved concavely inwardly).

Pronotum: Angular in outline, disk brownish black, lateral and posterior borders widely yellow. Surface somewhat uneven. Lateral edges smooth, nearly straight, posterior angle rounded. Anterior edge between eyes essentially straight, posterior edge bow-shaped. Venter with weak median sternal keel, large coxal cavities and coxae, and propleural flaps widely separated by coxal cavities. Pronotal ratios are: (1) Width between anterior angles to width between posterior angles 35: 60 (58%); and (2) median length to greatest width 20: 60 (33%).

Scutellum: Large, blackish, shiny; ratio of three sides, anterior and two laterals 35: 25: 25.

¹Biological Society of Nevada, Verdi, Nevada 89439.

Hemelytra: Translucent brownish; claval sutures distinct; membranes very large, comprising almost half hemelytral length and milky transparent. Opaque region microroughened but shiny. Embolium indistinctly delineated, the inner margin discernible and apparently extending caudally to intersect outer hemelytral edge so that posterior emboliar border is not at right angles to the long axis of the body; outer edge weakly flared externally about at midline; ratio of length-to-width 31:4 (13%). Hemelytra reaching caudally beyond tip of abdomen; connexival edge barely exposed in anterior half of abdomen. Wings fully functional.

Venter: The prothoracic venter has been discussed above. Meso- and meta-thoracic ventra blackish, as is the abdomen. Connexiva not distinguishable, posterior abdominal angles non-spinose. Abdominal segment I with a prominent, whitish, narrowly elongate static sense organ (*statexta*) near external edge; spiracles on segments II, III, IV and V each in form of a short series of transversely-arranged dots. Female subgenital plate narrowing rather sharply to an almost pointed tip.

Legs: *Proleg* — Coxa large, angularly-elongated. Trochanter prominent. Femur moderately incrassate, flattened, ratio of length-to-width 30:15 (50%), length 1.1 mm. Tibia long, narrow, tubular, bearing at its tip a two-segmented tarsus terminating in two small claws.

Mesoleg — Coxa and trochanter similar to proleg. Femur intermediate between the predatory incrassation of profemur and the elongated ambulation of metafemur, but not definable as incrassate; dense row of conspicuous yellow hairs on inner or posterior border; ratio of length-to-width 29:10 (34%), length 0.9 mm. Tibia long, narrow, tubular, slightly widening distally, heavily beset with large, yellow spines, these clustered rather solidly at distal end; ratio of length-to-width 25:3 (12%), length 0.85 mm. Tarsus 3-segmented, first segment minute, remaining two long, tubular, terminating in two prominent claws.

Metaleg — Much longer than other legs. Coxa and trochanter larger versions of mesoleg. Femur elongate, flattened, slightly bowed but not swollen as much as mesofemur; ratio of length-to-width 38:10 (26%), length 1.2 mm. Tibia long, narrow, rounded, slightly widening distally, sparsely spined, fringe of long swimming hairs on inner margin; ratio of length-to-width 33:5 (17%), length 1.1 mm. Tarsus very long and narrow, as long as tibia and consisting of 3-segments, the first minute; with a thick brush of swimming hairs on inside edge, and terminating in two large claws.

Type Locality and Etymology: Holotypic female, allotype and one paratype from: East India, Assam, Kohara, Kaziranga, 1959 Oct. 7, E. S. Ross and

D. Q. Cavagnaro, 110 m. Deposited in the California Academy of Sciences. The name *pygmaeus* is appropriate for this is the smallest of all known *Aphelocheirus*.

Comparative notes: *Aphelocheirus pygmaeus* is virtually unique in the family by size alone. I know of nothing else which even approaches it in this respect. In fact, it bears more superficial resemblance, on this basis, to the naucorid genus *Potamocoris*, than it does to other aphelocheirids.

Aphelocheirus nathani, new species

Figure 2

General: This description is based on the micropterous form as being the more common, with comparisons, in appropriate places, with the winged form. Lighter in color anteriorly, the darker abdomen lighter along edges. Winged form darker mainly due to blackish hemelytra and more color development on pronotal disk. Venter yellowish, with no significantly darker areas. Winged form darker ventrally. Size 9.5 by 6.5 mm (winged form 9.5 by 5.75 mm).

Head: Shiny, smooth, yellow except for diffuse brownish posteriorly. Keystone-shaped, broadly and moderately protuberant between eyes in anteclypeal region. Eyes darker, inner and outer margins subparallel, the *hyperocche* angle prominent

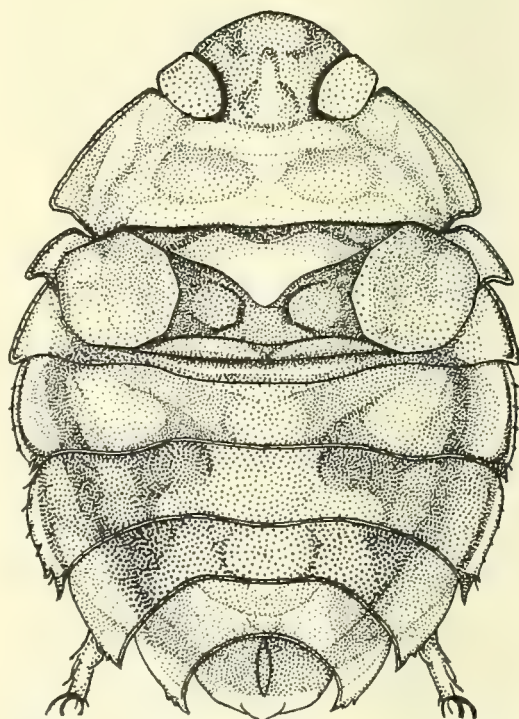


Figure 2. *Aphelocheirus nathani*, new species, holotypic female, micropterous form.

anteriorly, eyes essentially flush with general surface. Labrum prominent, broad and weakly pointed, ratio of length-to-width 16: 22 (73%). Head ratios are: (1) Total median length-to-width (including eyes) 65: 78 (83%) across hypercheal angles, (excluding eyes) 65: 55 (85%) anteriorly; (2) anterior distance between eyes to posterior distance between eyes 55:40 (73%); and (3) anterior distance between eyes to inner eye length 55: 40 (73%).

Pronotum: Yellow, with two diffuse brown areas centrally, surface shiny but weakly roughened. Posterior border double-angulate, the outer angle being the usual posterolateral one, the inner angle being a moderate, caudally-directed angulosity of the border; neither angle long or sharp. Lateral border smoothly curved; percent of curvature (as viewed perpendicularly to the frontal plane of section of the specimen as a whole) about 15 (68: 10). Venter yellow, coxal cavities large, median area moderately keeled. Internal propleural flaps widely separated by coxal cavities. Ratios are: (1) Width between anterior angles to width between posteroexternal angles 43: 92 (47%); (2) width between anterior angles to width between postero-internal angles 43: 73 (59%); (3) median length to greatest width 25: 92 (27%); and (4) median length to parallel length from anterior angle to posterior border 25: 39 (64%).

Winged form with straighter lateral borders, angles closer together, less pronounced, appearing more as the two edges of a longer, single angle which had been cut across diagonally, thus producing two reduced angles. Pronotum longer, broader, the proportions being: (1) Width between anterior angles to width between posteroexternal angles (= widest part of pronotum) 43: 87 (49%); (2) width between anterior angles to width between posterointernal angles 43:78 (35%); (3) median length to greatest width 27: 87 (31%); and (4) median length to parallel length from anterior angle to posterior border 27: 39 (69%).

Scutellum: Short, broad, yellow with some diffuse brownish areas anteriorly. Ratio of three sides, anterior and two laterals, 55: 36: 36. In winged form, scutellum proportionally larger, darker, more rugose, ratio 50: 38: 38.

Hemelytra: Yellow, texture same as pronotum; rounded, abbreviated stumps not reaching midline and not reaching posterior border of first abdominal segment. Anterior region of embolium present, the outer angle being sharp and slightly recurved. Winged form with fully developed wings, blackish brown, texture different from pronotum, being smoother with widely scattered tiny blackish tubercles; claval and membranous sutures prominent, the membrane distinct; embolium well developed,

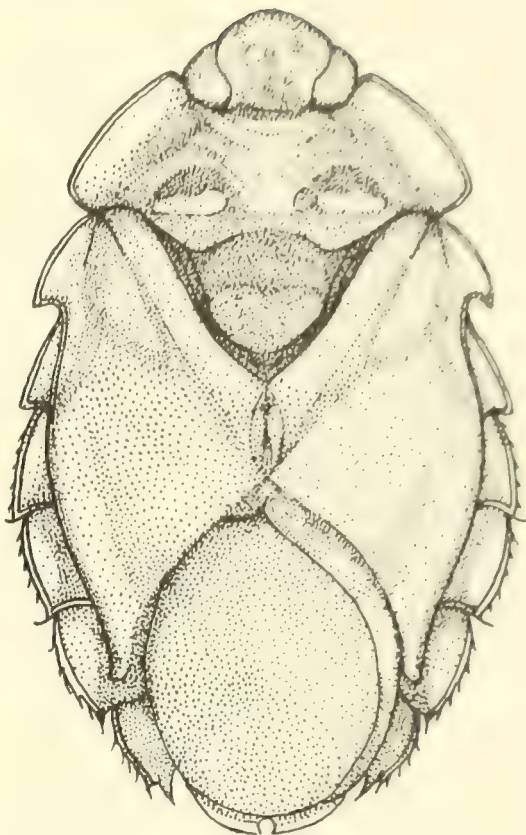


Figure 3. *Aphelocheirus nathani*, new species, paratype, macropterous form.

lighter laterally, long and narrow, the outer angle broad but distinct; embolium length-to-width 90: 20 (22%), but narrower than this would indicate since the width of 20 includes the outer angle; wings narrow, rather markedly exposing the connexival edge.

Venter: The prothoracic venter has been discussed above. Meso- and meta-thoracic ventra and abdomen yellow, darker in the winged form. Static sense organ prominent, elongated, small tip on posterior end; spiracles typically baliopic, the dots spreading laterally in all segments except I. Connexivum narrow, widening posteriorly in caudal segments, posterior angles sharp on all segments, becoming larger caudally. Female subgenital plate broadly wedge-shaped, narrowing sharply to a bluntly rounded tip.

Legs: *Proleg* — Coxa large, angularly-globular. Trochanter prominent. Femur weakly incrassate, flattened, well-furred along tibial closure edge; ratio of length-to-width 65: 24 (37%), length 2 mm. Tibia long, narrow, tubular, bearing a three-segmented tarsus whose first segment is minute, the remaining two elongate and terminating in two prominent claws.

Mesoleg — Coxa and trochanter similar to proleg except larger. Femur weakly incrassate, similar to profemur but larger, prominently haired along inner or posterior margin; ratio of length-to-width 63:20 (32%), length 2.1 mm. Tibia similar to protibia but proportionally broader, hairier and with a conspicuous armament of reddish spines, particularly along outer edge and a loose, transverse, terminal row; ratio of length-to-width 48:8 (17%), length 2 mm. Tarsus a larger edition of protarsus.

Metaleg — Much larger than pro- and meso-legs, with coxa more globular. Femur long, rather flat, not truly incrassate in any sense, thinly furred along posterior or inward edge; ratio of length-to-width 96:28 (29%), length 3 mm. Tibia relatively longer version of mesotibia, spined along edges and with a conspicuous fringe of long, yellow swimming hairs along internal or posterior border; ratio of length-to-width 90:9 (10%), length 3.1 mm. Tarsus large, much elongated, at least twice the length of mesotarsus and heavily equipped with swimming hairs inwardly.

Type Locality and Etymology: Holotypic female, allotype and 8 paratypes (2 being winged forms) from: South India, Madras, Anamalai Hills, Kadamparai, 1963 June, P. Susai Nathan, 1050 m; 2 micropterous paratypes from Anamalai Hills, Cinchona, Nathan, 1959 April, 1050 m, under debris of stream; 1 winged paratype from Coimbatore, Nathan, 1959 February. All specimens in the

collection of the Biological Society of Nevada, Verdi, Nevada. I am pleased to name the species after its collector, who has diligently sampled the naucorid fauna of his region.

Comparative notes: *Aphelocheirus nathani* appears to be related to the populations east, rather than west, of India, although the continuous and constant land masses to the west would appear a more likely continuum from which it could be derived. Lacking the distinct and prominent connexival spines of the *A. aestivalis* (Fabricius) 1803 group to the west, *A. nathani* is quite close to the Philippine species described by Usinger, *A. philippinensis* 1938 and *A. uichancoi* 1938, particularly the latter, which is about the same size. From *A. uichancoi*, *A. nathani* differs in the lighter color, somewhat smaller size and much different head proportions, *uichancoi* having the anteclypeal region much more extensively developed anteriorly between the eyes. The emboliar flare is also more pronounced in *nathani* and is longer. Connexival spines are somewhat more prominent in *uichancoi*.

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NEW SPECIES OF *POLYDORA* (POLYCHAETA: SPIONIDAE) FROM THE COAST OF CALIFORNIA

JAMES A. BLAKE¹ AND KEITH H. WOODWICK²

ABSTRACT: Four new species of *Polydora* are described. All species bore into calcareous substrata and occur in California, with one ranging as far north as British Columbia.

During the years 1961-70 numerous collections of intertidal polychaetes were made along the California coast by us. Examination of these collections has resulted in the finding of four new species. These are added to the genus *Polydora* which is already well represented in California. Hartman (1969) recorded 13 species in her "Atlas of the Sedentariate Polychaetous Annelids from California."

The four new species are described herein and information is presented on their distribution and general ecology. In addition, some information is

provided on reproduction in *P. elegantissima*.

The holotypes and one set of paratypes are deposited in the Allan Hancock Foundation, University of Southern California. Additional paratypes are deposited in the United States National Museum, Washington, D.C.

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Genus *Polydora* Bosc, 1802

***Polydora convexa*, new species**

Figure 1

Material examined: California: Santa Barbara, August 27, 1961 (1), from shells of hermit crabs; Avila, March 3, 1962 (8, TYPE), from shell of *Pododesmus macroschisma*; Morro Bay, October 24, 1961 (4), May 18, 1963 (13), from hermit crab shells and *Pododesmus*; Cayucos, June 28, 1961 (5), August 28, 1961 (13), December 19, 1961 (4), March 3, 1962 (4), July 3, 1962 (9), from hermit crab shells, encrusting sponge, holdfast of *Macrocystis*, and *Dodecaceria* colonies; Bodega Harbor, March 3, 1970 (3), from *Pododesmus*; Bodega Bay, September 30, 1970 (6), from Bryozoa, dredged in 20 m; Eureka (Trinidad Head), June 21, 1962 (10), from *Balanus* and hermit crab shells.

Description: Specimens of *P. convexa* from Bodega Harbor which were relaxed prior to preservation are largest in the collections and measure up to 30 mm in length and have over 200 segments. Specimens collected from other localities are somewhat smaller, ranging in size from 4.2 mm (45 segments) up to 15 mm (160 segments). Live individuals are light tan with occasional dark pigment on anterior body segments. This pigment may be a vestige of larval pigmentation.

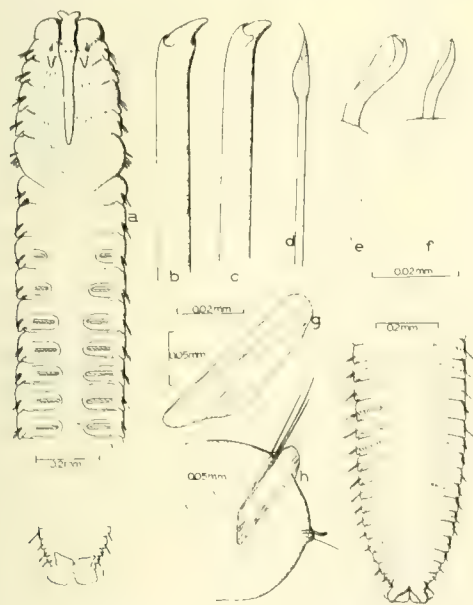


Figure 1. *Polydora convexa*, new species: a, anterior end in dorsal view; b-c, spines from setiger 5; d, pennoned companion seta from setiger 5; e, hooded hook from an anterior setiger; f, hooded hook from a posterior setiger; g, specialized notopodial structure from a posterior setiger; h, posterior setiger in anterior view with specialized notopodial structure in place; i-j, posterior segments in dorsal view.

The prostomium is bifid on its anterior margin (Fig. 1a). The caruncle extends to the posterior border of setiger 4. There is no nuchal tentacle. Eyes may be absent, but when present the four eyes are arranged in a trapezoidal manner with the posterior pair closer together and smaller than the anterior pair. The palps extend posteriorly only to setiger 10 in preserved specimens; in life they are longer and prehensile.

Setiger 1 has capillary setae in both noto- and neuropodia. Setigers 2, 3, 4, —, 6 and succeeding setigers have well-developed notopodial lobes preceded by posteriorly directed winged capillary setae arranged in three rows; an anterior row of short curved capillary setae, a second row of longer, less curved capillary setae, and a third row of long stout capillaries. The number of these setae per notopodium rapidly diminishes until in posterior segments only a few long slender capillary notosetae remain. In the posterior one-half of the body these capillary setae are accompanied in each notopodium by an unusual setal structure which is difficult to interpret (Fig. 1g-h). These structures do not protrude through the cuticle and resemble tight bundles of setal fibers. They are undoubtedly similar to the "organes en filières" of Claparède (McIntosh, 1915) found in *Spiophanes bombyx* Claparède. The neuropodia of setigers 2, 3, 4, —, and 6 have posteriorly directed capillary setae. Hooded hooks begin on setiger 7. They are bidentate (Fig. 1e) in anterior setigers with the secondary tooth gradually becoming smaller until it disappears entirely in posterior setigers. This results in a unidentate hook (Fig. 1f). The change-over from bidentate to unidentate is variable but usually takes place near the midbody region. In anterior setigers there are four or five hooks per neuropodium while in posterior setigers there are only 1-2 hooks. The hooks are accompanied by 1 or 2 very fine capillary setae throughout.

Setiger 5 is larger than preceding and succeeding setigers (Fig. 1a). The setae include a small bundle of dorsal geniculate setae lying anterior to a semi-circular row of alternating heavy spines (Fig. 1b-c) and smaller pennoned companion setae (Fig. 1d). The heavy spines are falcate and have a broad collar on the convex side (Fig. 1b-c). Ventral and posterior to the major spines is a small tuft of winged setae.

The slightly tapered and strap-shaped branchiae begin on setiger 8 (Fig. 1a). They are small at first and reach full size on about setiger 15. Branchiae are absent from the posterior two-thirds of the body.

The pygidium has four lobes (Fig. 1i, j). The dorsal pair are smaller than the ventral pair. The anus is located at the center of the lobes.

A structure similar in appearance to the "gizzard-like" structure previously described for *P. socialis* (Blake, 1969, 1971) was noted in *P. convexa*. It occurs at about setiger 18 on a 100 segment specimen. The structure does not appear to be as muscular or as well developed as in *P. socialis*. A similar type of structure was observed in *P. flava* by Carazzi (1893).

Remarks: *Polydora convexa* is unusual in having the accessory structure, in this case a flange, on the convex side of the heavy falcate spines of setiger 5. It is similar to *Polydora langerhansi* Mesnil (1896) declared *incertae sedis* by Fauvel (1927). Rioja (1925) had reported *P. langerhansi* from Madeira and later from Acapulco (Rioja, 1939, 1943). Mesnil reported no specialized notopodial setae in the posterior region, did not describe the pygidium, found no eyes, and made no mention of the unidentate hooded hooks in the posterior neuropodia. The spines of setiger 5 also resemble those of *P. armata* (Mésnil noted this for *P. langerhansi*) but members of the 2 species are not likely to be confused.

Ecology: *Polydora convexa* was found at Santa Barbara, Avila, Morro Bay and Cayucos in central California, and at Bodega Harbor and Trinidad Head in northern California. This species was found in many different habitats, including gastropod shells inhabited by hermit crabs. At Trinidad Head and Cayucos, *P. convexa* occurred in shells of *Tegula brunnea* with *Pagurus granosimanus*; *T. brunnea* with *P. samuelis*; *T. funebris* with *P. samuelis*; *Olivella biplicata* with *P. granosimanus*; and at Santa Barbara in shells of *O. biplicata* with *P. samuelis*. Other habitats include *Pododesmus macroschisma* shells; *Diadora aspera* shells; scrapings of rocks from surf zone; *Macrocystis pyrifera* holdfast; *Dodecaceria* colonies; and encrusting red sponges. It was found in the hermit crab habitat with a new species of *Boccardia* and was associated with *Polydora ciliata* and *B. columbiana* in nearly all of the above habitats and in several of them with *B. tricuspa*. Bryozoa dredged from 18 m off Bodega Head contained *P. convexa*, a new species of *Polydora*, described herein, and *Boccardia berkeleyorum*.

In *Pododesmus* shells at Bodega Harbor, *P. convexa* formed the branching type of burrow which is similar to that described by Evans (1969) for *P. concharum* which bores into shells of *Placopecten magellanicus* (Gmelin) in New England.

Distribution: California; Santa Barbara to Eureka.

***Polydora elegantissima*, new species**

Figure 2

Material examined: California; Tomales Bay,

March 30, 1970, intertidal from a hermit crab shell (1); Morro Bay, December 31, 1963, intertidal from shells of *Tivela stultorum* (Mawe) (8, TYPE); Malibu Beach, August 20, 1964. Subtidal in 2 m, from shells of hermit crabs (6).

Description: A complete specimen from Tomales Bay measures 31 mm in length, is 1 mm wide and has 170 setigerous segments. It was light tan (alive) with palps which were long and darkly pigmented along the margins of the ventral groove. There was no other body pigmentation. The specimen was first seen as it extended the long black palps from the shell of the hermit crab. The palps contracted greatly upon preservation. The holotype comes from Morro Bay, is incomplete, has 280 segments and is 44 mm long.

The prostomium is divided into two widely divergent lobes which on the Tomales Bay specimen resemble anterior horns (Fig. 2a). The caruncle extends prominently back to setiger 3 or 4 and thereafter continues as a low nuchal ridge for 30 or 40 segments; it may be indistinct on setiger 5. There are no eyes.

Setiger 1 has capillary setae in noto- and neuropodia. Setiger 2, 3, 4, —, 6 and succeeding setigers contain spreading fascicles of winged capillary notosetae arranged in 3 rows, each row with progressively longer setae. In far posterior setigers these setae diminish in number and length. There are no specialized posterior spines. The notopodial lobes of setiger 1 are shorter and more finger-like than those of 2, 3, and 4, which are large and auriculate. The lobes of setiger 6 and following setigers are shorter and more finger-like, the length gradually diminishing in middle and posterior setigers. The neuropodial lobes of setiger 2, 3, and 4 are also ear-like, although smaller than the notolobes, and they also diminish in size posterior to setiger 6. The neuropodia of setiger 2, 3, 4, —, 6, 7, 8, and 9 contain spreading fascicles of winged capillary setae which are arranged in 2 groups; a large dorsal fascicle and a smaller ventral group. Replacement of the winged capillary setae with bidentate hooded hooks takes place over the next few setigers. Hooded hooks begin on setigers 10, 11, or 12, but usually on 11. There are 5-7 hooks per neuropodium and only a few capillary setae. These remaining capillary setae are derived from the smaller, more ventrally situated fascicle which occurs on setigers 6, 7, 8, and 9. The capillary setae are absent about setiger 18, but are present again in the posteriormost setigers. The hooks have no constriction on the shaft and retain the same structure throughout the length of the body (Fig. 2b).

Setiger 5 is modified and larger than other

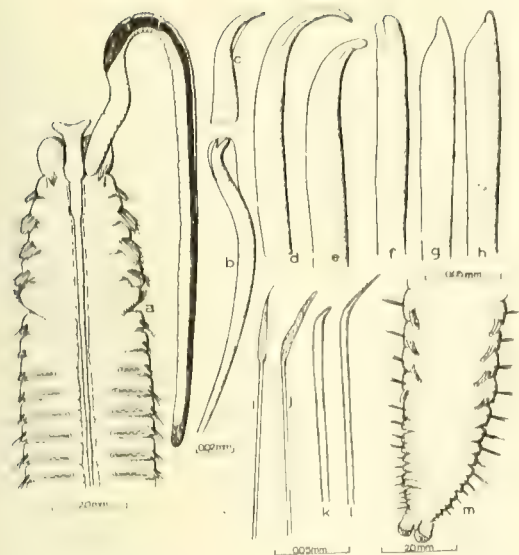


Figure 2. *Polydora elegantissima*, new species: a, anterior end in dorsal view; b, hooded hook; c-h, heavy spines from setiger 5 showing different angles and degrees of wear; i, superior dorsal seta of setiger 5; j, companion seta of setiger 5; k-l, neurosetae from setiger 5; m, posterior end in dorsal view.

setigers (Fig. 2a). The setae include a dorsal fascicle of pennoned setae (Fig. 2i) lying at the anterior end of a semicircular row of heavy modified spines (Fig. 2c-h) alternating with smaller pennoned companion setae (Fig. 2j). The deeper unworn heavy spines are sharply falcate and have a lateral sheath (Fig. 2c-d). Older worn spines are broader and more blade-like as a result of the erosion of the strongly falcate distal portion (Fig. 2g-h). Ventral to the row of heavy spines and companion setae is a neuropodial fascicle of stout geniculate setae (Fig. 2k-l). Some of these setae appear to be worn and have blunt frayed ends.

Branchiae begin on setiger 8 (occasionally 7) and continue to near the posterior end. They are relatively short and do not meet at the mid-line. The pygidium has 4 nearly equal lobes (Fig. 2m).

Reproduction: Egg capsules were collected with the Morro Bay specimens. Each capsule contained about 80 eggs and each egg measured about 150μ in diameter. Cleavage and larval movement were observed with non-pigmented early larvae following cleavage by about 45 hours. The culture subsequently became infected with bacteria.

Remarks: *Polydora elegantissima* is closely related to *P. commensalis*. It differs from them in the prostomium, caruncle, modified spines of setiger 5, and in the arrangement of the branchiae.

Distribution and Ecology: In Tomales Bay the

specimen was found in a shell of *Olivella biplicata* occupied by the hermit crab, *Pagurus granosimanus*. At Morro Bay it occurred in shells of *Tivela stultorum* and at Malibu Beach in shells with hermit crabs.

Polydora bioccipitalis, new species

Figures 3 and 4

Material examined: California; Malibu Beach (22 TYPE), August 20, 1964 from hermit crabs collected by James McHenry; Santa Barbara (1), July 30, 1965 from a shell of *Olivella biplicata* occupied by a hermit crab.

Description of the adult: Since both adults and post-larval juveniles are present in the collections and there are some features common only to the juveniles, the 2 groups will be treated separately. Adults measure up to 18 mm in length and have about 120 segments. There is no body pigmentation.

The prostomium is deeply notched on the anterior margin (Fig. 3a). The nuchal ridge extends past setiger 5 on most specimens and is visible on many anterior segments. On a few specimens a definite caruncle reaches only to the posterior margin of setiger 2. Two nuchal tentacles are present on large well-preserved specimens (Fig. 3a). The tentacles are well developed and one precedes the other. There are 4 eyes, rounded in shape; posterior pair is more closely spaced than the anterior pair. Palps are longer than those of *Poly-*

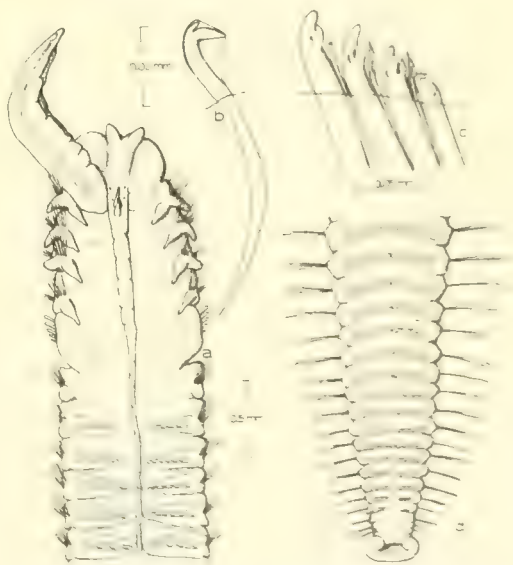


Figure 3. *Polydora bioccipitalis*, new species: a, anterior end in dorsal view; b, hooded hook; c, fascicle of heavy spines and companion setae from setiger 5; d, posterior end in dorsal view.

dora commensalis, but still relatively short when compared with most species of the genus. The Santa Barbara specimen was observed live and the first five setigers were narrower and showed less color (less blood) than succeeding setigers. When preserved, the anterior end contracted greatly and this combined with the shortening of the palps altered the specimen, causing it to appear fore-shortened. Setigers 1, 2, 3, 4 have well developed notopodial lobes.

Setiger 1 lacks notosetae. Setigers 2, 3, 4, —, 6 and succeeding setigers have fascicles of winged capillary setae. These setae are arranged in 2 rows with the longer setae in the posterior row. In posterior setigers the setae consist of a bundle of long laterally directed capillaries giving that part of the body a somewhat spinous appearance (Fig. 3d).

The neuropodia of setigers 2, 3, 4, —, 6, 7, 8 have spreading fascicles of winged capillary setae arranged in the same manner as the notosetae. Bidentate hooded hooks usually begin on setiger 9; however, on other individuals the hooks do not appear until setigers 10 to 14. Anteriorly there are 2 or 3 hooks accompanied by capillary setae. Posteriorly the hooks increase to 16 per neuropodium and the capillary setae disappear. The angle between the main fang and the secondary tooth is not great and there is only a faint suggestion of a constriction in the shaft (Fig. 3b).

Setiger 5 is larger than other setigers. The setae include a curved row of heavy spines alternating with pennoned companion setae (Fig. 3c). There is no anterior dorsal fascicle of setae and the ventral fascicle is lacking in the largest specimens, but is present in the smaller adults. The heavy spines are falcate and have 3 accessory structures. A thin fin or sheath lies between the distal end of the spine and a large accessory tooth. Both the tooth and fin may be so eroded as to be unrecognizable in older setae. A third accessory structure is a small triangular shaped tooth on the side of the spine. This small tooth can be seen only when the spine is viewed at certain angles.

The broad and flattened branchiae begin on setiger 7 and continue to near the posterior end (Fig. 3a, d).

The pygidium is a single thickened disk with a dorsal gap (Fig. 3d). The Santa Barbara specimen has in addition a slight ventral notch.

Description of the Juvenile: Post larval juveniles present in the collections range in size from 2.5 mm to 4 mm and from 28 to 36 segments. The striking difference between these juveniles and the large adults is the retention of larval pigmentation (Fig. 4a, c). The basic pattern of this pigment is the presence of lateral rows of black spots which begin on setiger 1 and continue to near the posterior end. Setiger 5 is unpigmented. A central row of chromatophores is found on the middle segments of the body and continues to the posterior end. Scattered pigment on the dorsal surface of setiger 7 and succeeding setigers suggests that in larvae the central row of chromatophores appeared on more anterior segments. Some individuals have additional pigment spots on the peristomium and pygidium. The pygidial pigment may form 2 dark spots on either side of the dorsal gap.

The anterior margin of the prostomium is broad on the small juveniles but shows signs of a bifurcation on the larger individuals. The nuchal ridge extends into setiger 2. Only one nuchal tentacle was found in juveniles (Fig. 4a). This suggests that the development of the two nuchal tentacles may be related to the age of the specimen and the posterior growth of the nuchal ridge or caruncle. The anterior pair of eyes tend to be cup-shaped in the juveniles.

Setation patterns are similar in juveniles and adults. The hooded hooks do not exceed 7 per neuropodium. Capillary setae are retained with the hooks on a greater number of setigers.

In juveniles there are two additional setal types found among the modified spines of setiger 5 (Fig. 4b). The first is a large curved spine with no accessory structures. The second is a more slender,

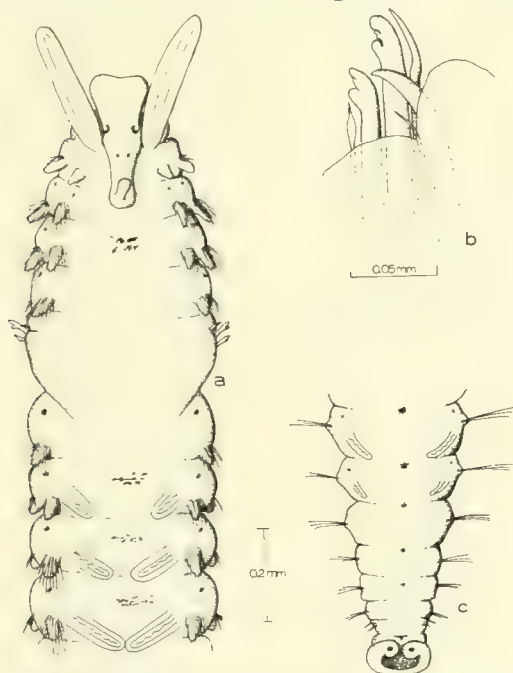


Figure 4. *Polydora bioccpitalis*, new species, juvenile: a, anterior end in dorsal view; b, group of setae from setiger 5; c, posterior end in dorsal view.

sharply hooked seta. The remaining heavy spines are as in the adults. A similar situation has been found in other polydorids (Blake, 1969) and it is suggested that the two additional setal types are hold overs from the larvae. The heavy larval setae are the first to be formed and are among the first to be worn down and replaced. Replacement is with the type of spine described for the adult. The branchiae and pygidium are as described for the adult.

Remarks: *Polydora biocipitalis* is unusual in the possession of two nuchal tentacles. *Polydora maculata* (Day, 1963) is the only other species of the genus which is known to have this feature, although several species have one nuchal tentacle. *Polydora maculata* is similar to *P. biocipitalis* in other characteristics as well, including the lack of notosetae on setiger 1, the appearance of hooded hooks on setiger 9, and the lack of dorsal and ventral fascicles on setiger 5. The two species differ in the structure of the heavy spines of setiger 5 and the length of the nuchal ridge. The heavy spines of *maculata* have only a lateral flange whereas, *biocipitalis* has three separate structures including two teeth and a flange.

The morphology of *P. biocipitalis*, especially the juveniles, is similar to the description of *P. punctata* from El Salvador (Hartmann-Schröder, 1959). That species was described from juveniles which resemble those of *P. biocipitalis* but the nuchal tentacles are not described nor figured. Further, the small lateral tooth of the specialized spines was not described.

Distribution and Ecology: At present, *Polydora biocipitalis* is known only from southern California at Malibu Beach and Santa Barbara. The species was found in gastropod shells occupied by the hermit crab, *Pagurus hirsutiusculus*. The shells included *Ocenebra poulsoni*, *Olivella biplicata*, *Murex gemma* and *Polinices reclusianus* at Malibu Beach where the species was found in association with other polydorids including *P. elegantissima*, *P. commensalis*, and *Boccardia tricuspa*. At Santa Barbara *P. biocipitalis* was found in a shell of *Olivella biplicata* occupied by *Pagurus hirsutiusculus* where it formed a shallow burrow which was covered dorsally with silt and mucous. This type of burrow is also formed by *P. commensalis* (Blake, 1969). *Polydora commensalis* is known to be a commensal of hermit crabs and since *P. biocipitalis* has a similar habitat and burrow, it seems possible that *P. biocipitalis* may also have a commensal relationship with hermit crabs. Other polydorids found in this habitat at Santa Barbara included *B. proboscidea*, *P. commensalis*, and *P. ciliata*.

Polydora pygidialis, new species

Figure 5

Polydora ciliata Berkeley and Berkeley, 1936: 4, 1952: 19-20 (not Johnston, 1838)

Material examined: California: Santa Barbara August 27, 1961 (4), from inner harbor piling material; Avila, March 3, 1962 (3), from hermit crab shells; Morro Bay, October 24, 1961 (23) May 18, 1963 (6); Cayucos, June 28, 1961 (5) August 28, 1961 (23, TYPE), December 19, 1961 (19), July 3, 1962 (1), from hermit crab shells, keyhole limpet shell, and piling material; Bodega Bay, September 28, 1970 (10), from bryozoa dredged from 18 m. British Columbia; Departure Bay, circa 1936 (4), from hermit crab shells (Berkeley and Berkeley, 1936).

Description: The individuals of this species are very slender. A specimen 9 mm long and having 100 segments is less than 0.5 mm in width. The anterior and posterior ends are slightly dusky in appearance but there is no strong body pigmentation.

The rounded prostomium (Fig. 5a) continues posteriorly as a narrow caruncle to the posterior margin of setiger 2. Palps on preserved specimens extend posteriorly to about setiger 10. Eyes may be absent but when present, the number is variable to a maximum of four. The anterior pair are widely-spaced and cup-shaped; the posterior pair are close

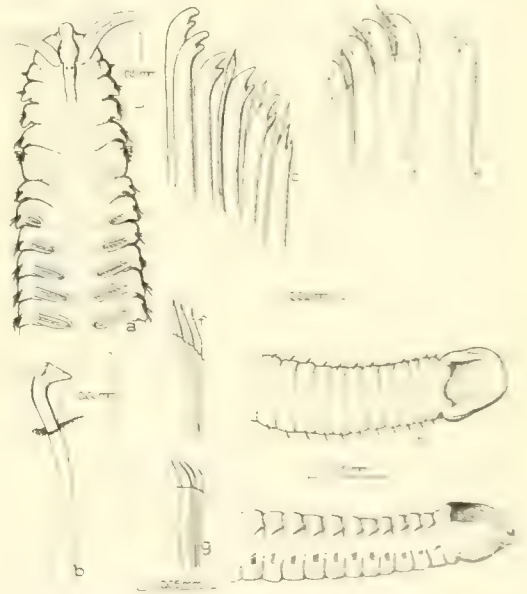


Figure 5. *Polydora pygidialis*, new species: a, anterior end in dorsal view; b, hooded hook; c-d, fascicles of heavy spines and companion setae from setiger 5; e, individual heavy spine from setiger 5; f, superior dorsal setae from setiger 5; g, neurosetae from setiger 5; h, posterior end in dorsal view; i, posterior end in lateral view.

together and irregularly shaped. In some specimens only the anterior pair are present.

Setiger 1 lacks notosetae but has a small conical notopodial lobe (Fig. 5a). The neuropodium of that setiger has a small fascicle of slender capillary setae and a bluntly rounded lobe. Setigers 2, 3, 4, —, 6 and succeeding setigers have well developed posteriorly directed spreading fascicles of winged capillary notosetae in two rows; setae of anterior row are shorter and slightly bent. This same general setal arrangement persists throughout the length of the body. There are no specialized posterior notosetae. The neuropodia of setigers 2, 3, 4, —, and 6 include fascicles of winged capillary setae. Bidentate hooded hooks begin on setiger 7 (Fig. 5b) and are not accompanied by capillary setae. There are four or five hooded hooks anteriorly with an increase to 10 in median setigers and a reduction to the original number posteriorly. The main fang of the hook is almost at a right angle to the shaft which has a constriction about one-half the way down its length (Fig. 5b).

The modified fifth setiger contains three groups of setae; a superior dorsal bundle of heavy, pointed setae (Fig. 5f), a curved row of large modified spines and alternating pennoned companion setae (Fig. 5c-d), and a reduced neuropodial fascicle of small, pointed setae (Fig. 5g). The heavy spines are falcate and have a large lateral accessory tooth whose apex curves back toward the main axis of the spine (Fig. 5c-d). The branchiae which begin on setiger 7 are flattened but are fingerlike in outline (Fig. 5a). They are short on anterior setigers but increase in length and nearly meet at the mid-line on about setiger 15. They are absent from the posterior one-third of the body.

In living specimens the pygidium is strongly scoop-shaped (Fig. 5h-i). Preservation may alter in part the shape of the scoop but the broad terminal end characteristic of the species remains easily identifiable.

Remarks: *Polydora pygidialis* is most closely related to *P. rickettsi* Woodwick (1961) from Lower California. It is distinguished from that species by the length of the caruncle, structure of the pygidium and the modified spines of setiger 5. In California, *P. pygidialis* is easily confused with *P. websteri* with which it may occur. The new species is distinguished from *P. websteri* in that the latter has a bifid prostomium, and the modified spines of setiger 5 have only an accessory flange. *Polydora pygidialis* is also similar to *Polydora limicola* Annenkova but in the latter the prostomium is vaguely incised and more importantly the palps are crossed by four or five bars of black pigment (Hartman, 1961).

Ecology: *Polydora pygidialis* was taken at Santa Barbara, Avila, Morro Bay and Cayucos in southern and central California. Most specimens were found in hermit crab shells, especially from the *Tegula funebris*/*Pagurus granosimanus* relationship. It was also found in piling material in the warmer waters of the inner harbor at Santa Barbara and the more open pilings in the colder waters at Cayucos. It was commonly associated with *Boccardia columbiana*. In the piling material from Cayucos it was also associated with *Polydora websteri*, a morphologically similar species. Bryozoa dredged from 18 m off Bodega Head contained *Polydora pygidialis*, *P. convexa*, and *Boccardia berkeleyorum*. *Polydora pygidialis* is a boring and/or nestling form. Egg capsules were found with the Bodega Bay material in September. The larvae are currently being studied by the first author.

Distribution: California (Santa Barbara) to British Columbia (Departure Bay).

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A NEW SPECIES OF *HUNTEROTREMA* (DIGenea: CAMPULIDAE)
FROM THE AMAZON RIVER DOLPHIN (*INIA GEOFFRENSIS*)

MURRAY D. DAILEY¹

ABSTRACT: A new species of *Hunterotrema* (Digenea: Campulidae) is described from the lungs of the Amazon river dolphin (*Inia geoffrensis*). It differs from the single species in this genus, *H. caballeri*, in body size, the lack of cuticular spines, placement of genital pore, and size of cirrus sac.

During investigations on marine mammal helminths, numerous lung trematodes taken from the Amazon river dolphin (*Inia geoffrensis*) were given to me for identification by Dr. Sam Ridgway, Naval Undersea Research and Development Center, Point Mugu, California. The specimens were found to be similar to, but much larger than, *Hunterotrema caballeri* McIntosh 1960. McIntosh (1960) described *H. caballeri* from 3 entire worms and 2 fragments of 2 additional specimens. The type material and additional specimens were obtained on loan from the USNM Helminth Collection, Beltsville, Maryland. A comparison of those 6 specimens not designated as part of the type-series (USNM Helm. Coll. Nos. 56921, 56922) with this material indicated a similarity between these forms. Both groups differed from *H. caballeri* sufficiently to warrant a new species description.

The worms from Dr. Ridgway had been fixed in 10% formalin, whereas, those received from Belts-

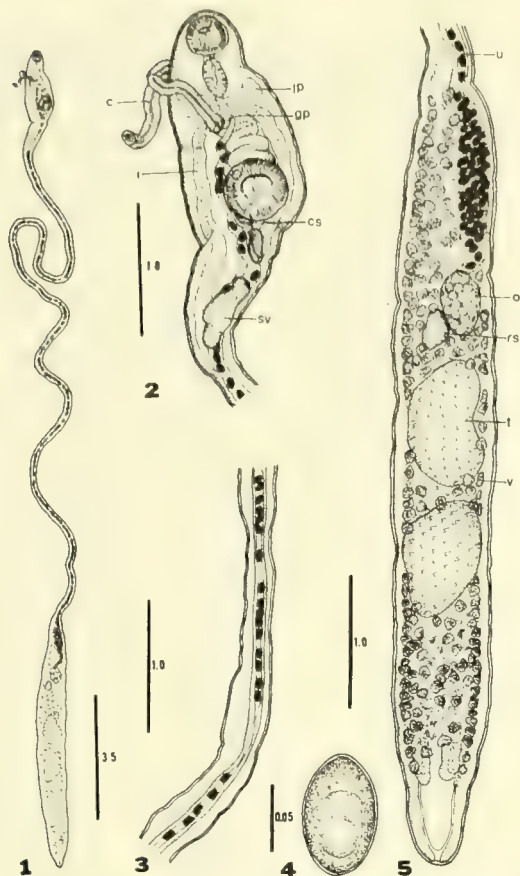
ville were in 70% ethanol. Whole mounts were stained in Semichon's carmine or celestine blue B, dehydrated in ethanol, cleared in xylene and mounted in piccolyte. Drawings were made with the aid of a drawing tube. All measurements are given in millimeters unless otherwise stated. Average measurements are presented with ranges in parentheses.

***Hunterotrema macrosoma*, new species**
Figures 1-5

Description based on measurements from 15 specimens.

Diagnosis: Body slender, elongate, 31 (24-36) long, with distinct forebody 3.7 (3.1-4.7), mid-body 19.6 (12.2-25.4) and hindbody 7.8 (6.0-9.8). Maximum body width 1.1 (0.74-1.46) at acetabular level, hindbody 1.0 (0.53-1.5) in region anterior testis

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Figures 1-5. *Hunterotrema macrosoma*, new species. Fig. 1. Ventral view of entire worm. Fig. 2. Forebody. Fig. 3. Mid-body. Fig. 4. Egg. Fig. 5. Hindbody. Abbreviations: c — cirrus; cs — cirrus sac; gp — genital pore; i — intestinal ceca; lp — lateral pockets of esophagus; o — ovary; rs — receptaculum seminis; sv — seminal vesicle; t — testis; u — uterus; v — vitellaria.

Spines lacking. Oral sucker, well developed, circular and subterminal 0.34 (0.30-0.40) in diameter. Prepharynx short, pharynx 0.32 (0.30-0.36) long by 0.19 (0.17-0.24) wide. Esophagus expanded anteriorly into two lateral pockets, 0.35 long (from midesophagus) by approximately 0.20 wide at ends (variable). Acetabulum, well developed, circular, 0.58 (0.50-0.67) in diameter. Cirrus long, unarmed. Cirrus sac 2.0 (1.8-2.1) long by 0.52 (0.43-0.60) wide, extending less than half its length posterior to acetabulum. Ovary oval, just cephalad to anterior testis, 0.33 (0.28-0.46) long by 0.35 (0.30-0.50) wide. Receptaculum seminis large, lateral to ovary. Seminal vesicle large, genital pore anterior to acetabulum just posterior to cecal bifurcation. Testes confined to median and posterior half of hindbody. Anterior testis 0.92 (0.65-1.15) long by 0.69 (0.48-0.98) wide. Posterior testis 1.03 (0.75-1.29) long by 0.71 (0.52-0.88) wide. Vitellaria, uniformly distributed, confined to hindbody,

extending from posterior end of intestinal caeca to anterior constriction of hindbody. Uterus coiled immediately anterior to ovary, then straightens to run as a sinuous tube to genital pore. Eggs oval 108μ (105-112) by 62μ (58-66).

Host: Inia geoffrensis

Location: Lungs

Locality: Amazon river basin, Leticia, Columbia and Iquitos, Peru.

Holotype and Paratypes: USNM Helm. Coll. Nos. 71583 (holotype), 71584, 56921, 56922.

DISCUSSION

Currently the genus *Hunterotrema* is represented by a single species, *H. caballeroi* McIntosh, 1960. *Hunterotrema macrosoma* differs from *H. caballeroi* in the following characters: (1) length and width of body (*H. caballeroi* 13.07 long by 1.64 maximum width); (2) lack of cuticular spines (*H. caballeroi* heavily spined from anterior to region of reproductive organs); (3) placement of genital pore (immediately anterior to acetabulum in *H. caballeroi*); (4) cirrus sac not extending more than half its length posterior to acetabulum as in *H. caballeroi*.

Since both familiar (Campulidae Odhner, 1926) and generic diagnosis included the presence of spines, an emendation to both is proposed to include *H. macrosoma* and should read "Cuticular spines present, or lacking."

Woodard *et al.*, (1969) described the pathology of pulmonary trematodiasis in an Amazon river dolphin from Iquitos, Peru. The photograph and measurement (printed, in error, as "approximately 250 mm in length" but corrected by Dr. Stephen Zam, University of Florida [pers. comm.] to be 25 mm) indicates the trematodes involved in the report were *H. macrosoma*, not *H. caballeroi*.

ACKNOWLEDGMENTS

I would like to express my appreciation to Sam Ridgway of NUC for collecting the specimens, and to the late W. W. Becklund for the loan of specimens from the USNM Helminthological Collection, Beltsville, Maryland. My sincere thanks to Lorraine Peterson and Barry Hill for their technical help.

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A NEW SUBSPECIES OF FUNNEL-EARED BAT (*NATALUS STRAMINEUS*)
FROM WESTERN VENEZUELAOMAR J. LINARES¹

ABSTRACT: A new subspecies of the funnel-eared bat *Natalus stramineus* is described from a cave in the Guasare river, Zulia, Venezuela. On the basis of palatal structure, the 3 recognized subspecies of *N. major* are assigned to *N. stramineus*. The species status of *N. tumidirostris* and its possible synonymy with *N. stramineus* are also discussed. Additional records of *N. t. continentis* from northern Venezuela are included.

In October 1967, an expedition of the Venezuelan Society of Speleology collected four specimens of a unique funnel-eared bat in a cave in the state of Zulia, Venezuela. These proved to be the first specimens of *Natalus stramineus* taken in Venezuela and northern South America. Comparison with material from Central America indicates that the Venezuelan bats represent a distinct subspecies, which is named and described below.

***Natalus stramineus tronchonii*, new subspecies**

Holotype: An adult male, alc. with skull, Biology Museum, Central University of Venezuela, MBUCV 1-1578, collected by J. A. Tronchoni (original number L-281) from Gavilanes cave (Zu-1, Soc. Venezolana Espel., 1968: 113-118), Guasare river, Zulia, Venezuela, 183 m, 20 October 1967.

Paratypes: Three adult females, alc. with skulls, MBUCV 1-1577, 1-1579 and 1-1580 of the same locality, date and collector.

Distribution: Known only from the type locality.

Diagnosis: A small subspecies with the posterior border of the bony palate deeply emarginate to the level of the last molar. Very similar to *N. s. mexicanus* Miller [= *N. s. saturatus* Dalquest and Hall, 1949], but smaller, and morphological characters intermediate between *tumidirostris* and *stramineus*.

Description: Body size small (forearm 39.7 mm; greatest length of skull 16.1 mm). Dorsal coloration after one year in alcohol (capitalized color terms after Ridgway, 1912) Cream Buff, tips of hairs gradually darkened to a Pale Drab, underparts more yellowish than back. Vibrissae abundant and conspicuous on snout. Ears and lips grayish. Membranes, feet and legs, dark brown. Other somatic characters as in *N. stramineus*. Skull strictly similar to that of *stramineus* type, but with a palate intermediate in size between *stramineus* and *tumidiro-*

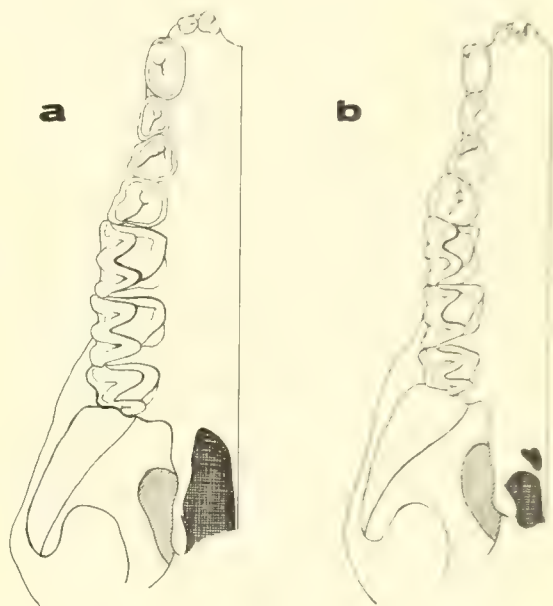


Figure 1. Palatal emargination and dentition of upper right jaw of: a, *Natalus stramineus tronchonii* (MBUCV 1-1578, ♂—holotype), and b, *Natalus stramineus mexicanus* (TCWC 8507, ♀).

rostris. Upper molar with the hypocone widest lingually. The differences in the palate and dental characters between *N. s. tronchonii* and *N. s. mexicanus* are shown in Figure 1.

Measurement: The holotype and the paratypes are similar (Fig. 2; Table 1).

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TABLE 1. Measurements (mm) of *Natalus stramineus tronchonii* from Venezuela compared with selected measurements of *Natalus stramineus mexicanus* from Mexico, Nicaragua and Guatemala.

	<i>N. s. tronchonii</i>				<i>N. s. mexicanus</i>		$\bar{X} \pm 1SD$
	1577 ♀	1578 ¹ ♂	1579 ♀	1580 ♀	n	Range	
Total length (body + tail)	97.0	97.0	92.0	100.0	—	—	—
Length of tail	52.0	51.0	46.0	53.0	—	—	—
Hind foot	8.0	8.5	8.0	8.5	—	—	—
Ear from meatus	14.0	14.5	13.0	14.0	—	—	—
Forearm	38.3	39.7	37.1	38.3	10	(36.9-39.8)	38.25 ± 0.85
Third finger, metacarpal	35.0	36.6	34.8	36.1	10	(34.4-37.5)	35.75 ± 1.00
first phalanx	16.4	15.9	15.3	15.7	10	(14.0-17.0)	15.35 ± 0.70
second phalanx	21.8	21.6	20.7	21.7	10	(19.3-22.3)	21.14 ± 1.04
Fourth finger, metacarpal	35.2	35.2	33.8	35.2	10	(33.3-37.3)	35.20 ± 1.12
first phalanx	10.0	9.0	9.6	9.4	10	(8.4-10.4)	9.16 ± 0.61
second phalanx	9.9	10.6	9.7	10.3	10	(9.5-10.6)	9.90 ± 0.34
Fifth finger, metacarpal	35.3	34.9	34.2	34.6	10	(33.4-37.3)	34.93 ± 1.33
first phalanx	9.6	8.9	9.1	8.9	10	(8.3-10.1)	9.06 ± 0.55
second phalanx	10.4	10.5	10.5	10.4	10	(9.5-11.4)	10.26 ± 0.67
Skull,							
greatest length	15.5	16.1	—	15.9	10	(15.4-16.4)	16.02 ± 0.39
condylo-basal length	14.4	14.9	—	14.8	10	(14.2-15.2)	14.73 ± 0.32
condylo-canine length	14.0	14.3	—	14.3	9	(14.2-14.9)	14.48 ± 0.24
basal length	13.1	13.5	13.1	13.4	10	(13.3-13.9)	13.54 ± 0.20
palatal length	7.7	7.0	7.8	7.7	10	(8.7-9.6)	9.02 ± 0.29
zygomatic width	7.7	8.1	7.7	—	10	(7.9-8.3)	8.11 ± 0.19
width of braincase	7.4	7.7	7.7	7.4	10	(7.5-8.0)	7.73 ± 0.14
height of braincase	6.1	6.1	—	5.9	10	(6.1-6.5)	6.22 ± 0.12
length of foramen magnum	3.0	3.4	—	2.9	10	(2.5-3.2)	2.67 ± 0.20
width of foramen magnum	3.3	3.6	—	3.6	9	(3.2-3.9)	3.43 ± 0.20
mastoidal width	7.0	7.3	—	7.1	9	(7.3-7.5)	7.41 ± 0.09
interorbital width	3.3	3.2	3.2	3.2	10	(2.8-3.1)	3.00 ± 0.10
width across molars	5.0	5.2	5.1	5.2	9	(5.1-5.3)	5.26 ± 0.06
width across canine	—	3.5	3.4	3.5	9	(3.5-3.8)	3.61 ± 0.10
upper toothrow, c-m ³	6.5	6.8	6.5	6.7	9	(6.8-7.0)	6.86 ± 0.08
lower toothrow, c-m ₃	7.0	7.1	6.8	7.1	9	(7.2-7.5)	7.33 ± 0.08
length of mandible	11.7	12.0	11.8	11.9	8	(11.4-12.5)	11.79 ± 0.32

¹ holotype

Comparison and discussion: There are no external characters by which *N. stramineus* can be distinguished from *N. tumidirostris*. In cranial characters *N. s. tronchonii* can always be recognized by the small, swollen maxillary bones and semi-emarginated palate.

The characters of this population give rise to new doubts about the 3 recognized species of the subgenus *Natalus* (Dalquest, 1950). These 3 species are very similar (Goodwin, 1959); *major* is the largest (Jamaica, Cuba, Dominican Republic and Haiti), *tumidirostris* is intermediate in size (northern Venezuela, Curacao, Trinidad and Colombia) and *stramineus* is the smallest (Mexico, Central

America, western Venezuela and northeast Brazil). The size differences in some cases are not significant and, in general, are no greater than 2 to 3 mm in all known forms. Recent comparisons of more than 40 specimens from Venezuela and the 18 from Trinidad (some of which were reported by Goodwin, 1959) have led me to concur with Goodwin (1959) and Handley (1966) in considering *N. stramineus saturatus* Dalquest and Hall a synonym of *N. s. mexicanus* Miller, and to place *N. tumidirostris haymani* Goodwin in synonymy with *N. t. continentis* Thomas.

On the basis of an analysis of the form of the palate, only 2 groups can be admitted: *stramineus-*

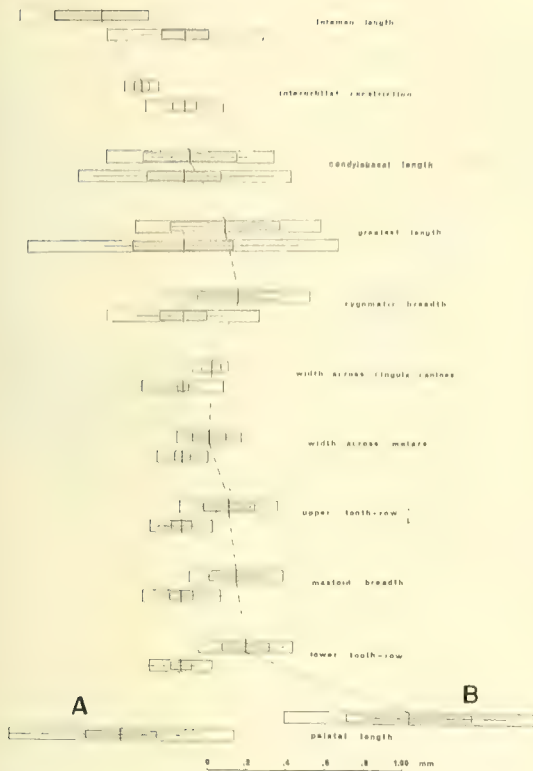


Figure 2. Comparisons of selected measurements of *Natalus stramineus mexicanus*, A (means connected by dotted line), and *N. s. tronchonii*, B (means connected by a dashed line). The means of measurements of the former have been arranged to form a base line for comparison with those of *N. s. tronchonii*. Horizontal lines indicate range, small boxes ± 1 standard error and large boxes ± 1 standard deviation.

major with a very short palate, and *tumidirostris* with a very long palate. The intermediate palate of the Venezuelan population poses the interesting question of a possible cline, and makes a careful revision of the subgenus necessary. Tentatively, I suggest that the 3 subspecies of *major* (Goodwin, 1959) be assigned to *stramineus*, thus bringing to 6 the known forms of this latter species.

Koopman (1968) assumes the presence of *N. stramineus* in the Lesser Antilles by way of South America. However, on the basis of this new criterion, it would be wiser to think of a mainland Neotropical center of origin, following a route from Yucatán (Mexico), Cuba, Jamaica, Hispaniola, to the Lesser Antilles; as the forms of *stramineus* have not been localized in northern South America. Goodwin (1959:4) mentions specimens from Brazil, Venezuela, and Trinidad, but he does not note any specific locality in either Venezuela or Trinidad.

Based on the criterion of palatal structure, it is more likely that *tumidirostris* is also a member of *stramineus*, thus reducing the subgenus *Natalus* to only one species. In this paper, I will retain *tumidirostris* as a full species which represents the maximum in the differentiation within the *stramineus-major* groups; more examples from South America should confirm or negate this thesis. A revision of the other species grouped in the various subgenera, and field investigations in the Greater Antilles, particularly Puerto Rico, would also provide new information concerning these delicate bats.

Additional specimens examined: Comparative material was kindly made available by the Texas Co-operative Wildlife Collection (TCWC), the American Museum of Natural History (AMNH), the United States National Museum (USNM), the La Salle Museum of Natural History (MHNLS), and the Museum of Natural Sciences, Caracas (MCNC). Specimens in the mammal collection, Biology Museum of the Tropical Zoological Institute (Central University of Venezuela), are designated by the abbreviation (MBUCV).

Natalus stramineus stramineus: ANGUILLA. Northside Estate (AMNH, 2).

Natalus stramineus major: DOMINICAN REPUBLIC. Barahona (AMNH, 2), Maniel Viejo (AMNH, 1).

Natalus stramineus jamaicensis: JAMAICA. St. Clair (AMNH, 3).

Natalus stramineus mexicanus: MEXICO. Chiapas: Cintalapa (TCWC, 2). Nayarit: Amatlán (AMNH, 8). Tamaulipas: El Pachon (AMNH, 5). GUATEMALA. Puerto Barrios (TCWC, 7); El Progreso (AMNH, 6). NICARAGUA. Rama (TCWC, 1).

Natalus stramineus tronchonii: VENEZUELA. Zulia: Guasare river, (MBUCV, 4).

Natalus tumidirostris continentis: TRINIDAD. Oropuche caves (MCNC, 1); Mt. Tamana (AMNH, 10). VENEZUELA. Carabobo: San Esteban (AMNH, 10). Arauca: Rancho Grande (MBUCV, 1); El Limón (MHNLS, 1). Miranda: Baruta (MHNLS, 1); El Hatillo (MBUCV, 3); Petare (MHNLS, 1); El Encantado (MBUCV, 44). MHNLS, 24. USNM, 7); Araira (MHNLS, 3); Virongo (MBUCV, 2); Capaya (MHNLS, 2). Falcon: Peninsula de Paraguaná (USNM, 20). Bolívar: Caicara (USNM, 15). COLOMBIA. San Gil. Cueva del Nitro (AMNH, 2).

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A NEW SPECIES OF *IPHITIME* (POLYCHAETA) FROM *CANCER ANTENNARIUS* (CRUSTACEA: DECAPODA)

JOHN PILGER¹

ABSTRACT: A new species of *Iphitime* is described from *Cancer antennarius*. Notes are given on the morphological criteria used in separation of the five species of the genus.

During fixation of a specimen of *Cancer antennarius* (Stimpson, 1856) at the Santa Catalina Marine Biological Laboratory, 2 specimens of a new species of *Iphitime* crawled out between the third maxillipeds of the host. These 2 specimens belong to a new species which is described below with notes on frequency of infection and some morphological features of the family.

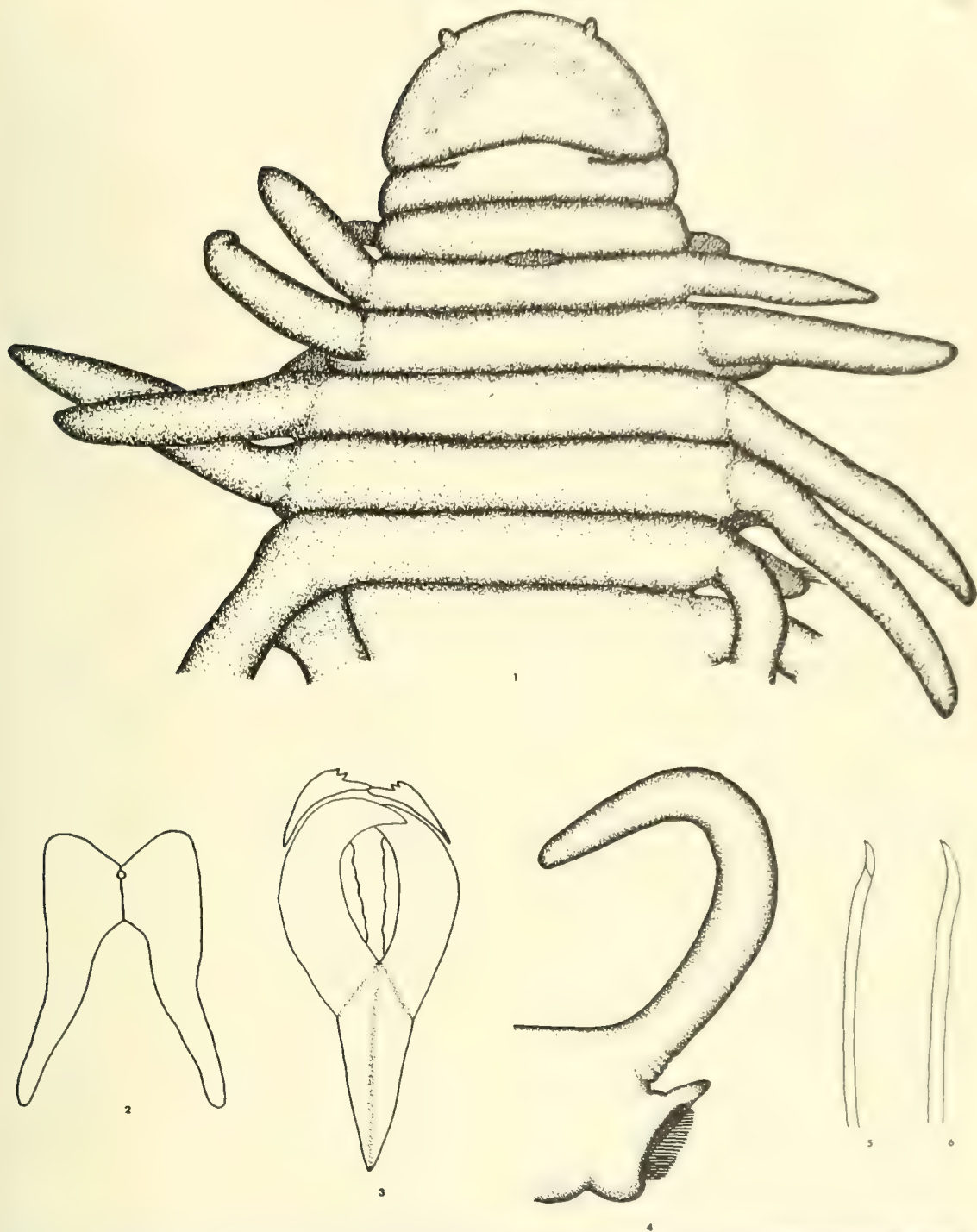
Iphitimidae Fauchald, 1970

The genus *Iphitime* was originally referred to the family Lysaretidae (Marenzeller, 1902) but was recently raised to familial status by Fauchald (1970). This separation was made because members of this genus possess branchiae, composite setae, two antennae, three paired maxillae, maximally, and they lack an unpaired maxillary carrier. The

lysaretids, on the other hand, lack branchiae, have simple setae, three antennae, five maxillae, and three maxillary carriers.

Fauchald (1970:118) states that iphitimids have only simple falcate unhooded setae. However, this should be expanded to simple and composite unhooded setae. In addition, the two peristomial segments noted by Fauchald (1970:118) as diagnostic of the family Iphitimidae should be broadened to one or two peristomial segments. This change in the familial definition is made to encompass the new species, which has only one peristomial segment. All species of *Iphitime* are found in the branchial cavities of decapod crustaceans (Fauchald, 1970). Hartman (1952) suggested that

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Figures 1-6. Fig. 1, Dorsal view of anterior end, X48; Fig. 2, Mandibles, removed from maxillary apparatus, ventral view, X110; Fig. 3, Maxillary apparatus, mandibles removed, ventral view, X110; Fig. 4, Median parapodium, anterior view, X21; Fig. 5, Composite falcate setae, X245; Fig. 6, Simple falcate setae, X245.

they may feed on small particles of food swept into the branchial cavity by respiratory currents. However, it should be noted that all species of *Iphitime*

have well-developed jaws for biting and chewing which suggests that they may parasitize the branchial tissue of the host.

***Iphitime holobranchiata*, new species**

Figures 1-6

Material: The specimens were taken from a large male *Cancer antennarius* (Stimpson, 1856) caught near Little Harbor, Santa Catalina Island, California. The holotype, measuring 48 mm, and one paratype (broken in two), 25 mm, are both deposited in the Allan Hancock Foundation. A number of individuals from an unknown locality measured from a few millimeters to 120 mm; all were found in the branchial cavity of the host crab.

Description: The 2 specimens measured 25 mm and 48 mm. Each had 175-200 setigerous segments. The color in life is pink-orange.

The prostomium (Fig. 1) is a rounded lobe with 2 small antennae. These extend beyond the outline of the anterior margin of the prostomium when viewed from above. A shallow depression curves around the anterior and anterolateral portions of the prostomium.

There is 1 peristomial segment. Between the prostomium and the peristomium is a narrow slit-like nuchal organ (Fig. 1).

The mandibles (Fig. 2) are fused medially in their anterior portion for about one-sixth of their entire length. A conspicuous hole is located in the anterior portion of this suture. The maxillary carriers (Fig. 3) are fused medially with their free edges extending dorsally to form a V-shaped structure. At their anterior margins they are fused with the large falcate maxillae I. Dorsal to this are the wavy-edged maxillae II. Distinct teeth are absent. Each maxillae III has 1 large and 2 smaller teeth.

The long branchiae are dorsolateral. Branchiae are first present from the second setigerous segment. Each is long and digitiform (Figs. 1, 4).

Parapodia (Fig. 4) consist of a small ventrolateral presetal lobe and a large dorsolaterally directed postsetal lobe. There are 5-7 composite falcate setae (Fig. 5) and about 29 simple falcate setae (Fig. 6) in each parapodium. All lack hoods. Eight acicula are present.

Discussion: In contrast to other species of *Iphitime*, *I. holobranchiata* has only 1 peristomial segment. All other species have 2. *Iphitime doderleinii*, *I. cuenoti*, and *I. paguri* all have more composite falcate setae than simple ones. The opposite situation exists in *I. holobranchiata* which has many more simple than composite falcigers.

Iphitime paguri and *I. holobranchiata* are the only 2 species in the genus with simple unbranched branchiae. In *I. holobranchiata* they are inserted dorsolaterally while in *I. paguri* they are dorsal. The specific name *holobranchiata* was chosen because it connotes simple, whole, unbranched branchiae.

All species have 3 maxillae except for *I. loxorhynchi* which has only 2. Maxillary formulas for all species are given in Table 1, which is expanded from Hartman (1952) by adding *I. holobranchiata* and diagnostic characters not contained in her table.

Distribution: *Cancer antennarius* ranges from British Columbia to Magdalena Bay, Baja California. Examination of the branchial cavities of live *C. antennarius* from southern California showed the infection frequency to be quite high. From the 30 individuals inspected 142 *I. holo-*

TABLE 1. Diagnostic characters of species in the genus *Iphitime*.

Name of Species	Total Length in mm	Host Species and Locality	Number of Setigerous Segments	Number of Peristomial Segments	First Presence of Branchiae and Character	Parapodial Components	Number of Maxillae	Maxillary Formulae
<i>I. cuenoti</i> Fauvel	7-12	<i>Maia squinado</i> <i>Portunus</i> spp. <i>Gonoplax angulata</i> <i>Macropodia longirostris</i> All from Europe	20-60	2	First; simple to divided, lateral	4-5 simple falcigers 20 composite falcigers	3	1+1-1+1-1+1
<i>I. doderleinii</i> Marenzeller	61	<i>Macrocheira kaempferi</i> Japan	185-210	2	First; simple and palmate, midlateral	14-15 simple falcigers Many composite falcigers About 4 acicula	3	1+1-1+1-1+1
<i>I. holobranchiata</i> , new species	25, 48 ¹	<i>Cancer antennarius</i> Southern California	175-200	1	Second; simple	29 simple falcigers 5-7 composite falcigers 8 acicula	3	1+1-0+0-3+3
<i>I. loxorhynchi</i> Hartman	60-70	<i>Loxorhynchus grandis</i> Southern California	200 or more	2	Second; simple to divided, lateral	26 simple falcigers 20 composite falcigers 6 acicula	2	1+1-0+4 (5)
<i>I. paguri</i> Fage & Legendre	7	<i>Gonoplax angulata</i> <i>Macropodia longirostris</i> <i>Portunus depurator</i> <i>Eupagurus bernhardus</i> All from Europe	86-90	2	Fourth; simple dorsal	1 simple falciger 7-8 composite falcigers	3	1+1-1+1-1+1

¹Measurements of holotype and paratype only.

branchiata were taken. The maximum number found in any one crab was 39.

Ecology: Small specimens commonly occupied the interlamellar areas of the phyllobranchs while larger ones were found on the walls of the cavity or on the surface of the branchiae. No visible damage to the gills was observed.

ACKNOWLEDGMENTS

I wish to thank the crew of the U.S. Naval Undersea Research and Development Center vessel Sea-See who collected the *Cancer* crab in which the polychaetes were found. Research facilities were provided by the Santa Catalina Marine Biological Laboratory, University of Southern California, and I would like to thank the staff for their encouragement.

Reference materials were furnished by Olga Hartman and the Allan Hancock Foundation Library. A very special thanks goes to Kristian Fauchald who provided me with equipment, information, criticism, and inspiration.

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TWO TYPES OF AGGREGATION GROUPING IN THE LARGE MILKWEED BUG, *ONCOPELTUS FASCIATUS* (HEMIPTERA: LYGAEIDAE)

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ABSTRACT: Two types of grouping behavior, parallel and linear groups, in the large milkweed bug *Oncopeltus fasciatus* (Dallas) seem to have survival value. Grouped bugs receive mutual benefit from the ability to perceive stimuli from more directions and are usually touching each other. Color pattern and uniformity of direction causes a striking pattern in aposomatic insects. A combination of the shape of the bugs, limited areas for grouping on the plant, and microclimates have influences on the type and shape of aggregations. Aggregation may also be influenced by the substrate, position of the heat or light source, and changing behavioral and physiological stages of the bug.

The milkweed bug, *Oncopeltus fasciatus* (Dallas), has a gregarious behavior that has been documented by Weiss and Dickerson (1921), Andre (1934), Beck, Edwards and Medler (1958), and Barrett and Chiang (1967a). Gregarious behavior in milkweed bugs is herein defined as the condition which exists when one bug is within one body length of another bug. When two bugs are of different sizes, the length of the larger bug is used as the measure between bugs.

Aggregation or grouping is a normal occurrence in the bugs and they spend the majority of their lives in close proximity to one another. A "normal" aggregation consists of grouped bugs seemingly oriented in almost every direction. The bugs may be in compact groups where there is much contact

between bugs or in loose groups where there is little contact.

OBSERVATIONS

Time-lapse pictures were taken of milkweed bugs grouped inside plastic containers. In the process of taking these pictures two grouping behavior patterns were observed (on the bottom of the container) which were different from normal aggregation. These two groupings have been observed on other substrates with varying conditions and are herein labeled "linear groups" and "parallel groups."

In a linear group the bugs will line up in com-

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binations of head to head, tail to tail, and head to tail so that their longitudinal axes line up in more or less one straight line. As many as 6 fifth instars, out of a population of 10, have been observed in this type of grouping. The line of bugs may be straight or it may curve slightly (Fig. 2).

In a parallel group the bugs will line up side by side, as if in a row. The longitudinal axes of their bodies will be parallel to one another. Their heads will usually be pointing in the same direction. As many as 5 bugs, out of a population of 10, have been observed in this type of grouping (Fig. 1).

Both linear, parallel, and combinations of these two types of groupings are found in the 5 instars and the adult stage. Linear and parallel groupings are usually a part of normal grouping activity, although they may appear attached appendicularly to a larger group. Both parallel and linear groups generally did not last longer than 20 minutes in the time-lapse experiments.



Figures 1-2. Fig. 1. Fifth instars in a parallel group. Notice contact between legs, antenna, and body. Fig. 2. Fourth instars in a linear group. Notice contact between forelegs, antenna, and head. Figures drawn from projected 16 mm color film. Line equal to 1 cm.

DISCUSSION

The explicit reasons for these types of grouping are not known, but there seems to be evidence for each of the following factors: copulation, protective coloration, physical properties of the milkweed plant, shape of the bugs, effect of light, temperature, physiological state of the bug, visual and tactile responses, and other external factors. Some of these factors will be briefly discussed in relation to survival value of the special kinds of groups previously discussed.

Copulation: Andre (1934) has described the method of copulation in the milkweed bug. When a male attempts to copulate with a female, the male usually forms a very short-lasting parallel group. After the male and female attach genitalia, they move into a position in which both longitudinal axes lie on the same line and their heads are pointing in opposite directions. This is a type of linear grouping. Other bugs were observed lining up with a copulating pair to form a linear group of 4 or

more bugs. Temporary parallel and linear groups may also be formed when a secondary bug attempts to mate with a copulating pair. A copulating pair in a linear group will gain the protective advantage of potentially perceiving stimuli from more directions than an individual bug.

Both types of groupings are related to mating positions. Parallel and linear groups occur in all 5 instars. Sexual behavior is probably not the only causative mechanism for this type of grouping since the instars are incapable of mating. The groupings may have influenced typical hemipteran mating behavior.

Protective coloration: A specific color or color arrangement, adapted for recognition of undesirable species, has been suggested as one means of protection for some insects by Ehrlich and Raven (1967) and Cott (1957). The bug is black with yellow to orange-red coloration. The percentage of black area increases with each succeeding instar. The pattern or color may be important in learning to avoid unpalatable bugs (Rettenmeyer, 1970). Gelperin (1968) stated, "The large milkweed bug, *Oncopeltus fasciatus*, served as the distasteful prey [for mantids]." The milkweed bug will exude a pungent fluid when disturbed.

Protection may be gained by easier recognition of large aggregations of aposematic animals (Cott, 1957). A group of aposematic bugs may gain some advantage by being grouped in the most compact possible type of grouping or by producing a more striking pattern incorporating uniformity of direction.

Grouping may be accomplished by normal compact grouping with some bugs on top of others. These layers will tend to cover up the empty spaces between the bugs and appear as a solid mass. Multiple layers of bugs have been observed in the field. Layers of bugs have also been observed in the laboratory. Barrett and Chiang (1967a) reported eight layers of bugs on a heat gradient. The layers of bugs may or may not be due to a lack of space. A pheromone may be involved in aggregation and group formation in the bugs.

An efficient covering of the plant may be produced by bugs lining up in parallel and linear combinations. Most bugs are found at angles to one another indicating other factors influencing group formation.

Physical properties of the plant: The relationship of bugs to the substrate, surface texture, horizontal and vertical surfaces, and available room for grouping are important in development of aggregations. *Asclepias fascicularis* is a glabrous milkweed, about 1 m tall, and found in dry places in cismontane California and other parts of the western United

States. Aggregations are common on the upper parts of the plant, but the bugs have been observed at the base of the plant at night, before flowering, and after the plant has started to die back. The highest population densities occurred after flowering or while the follicles were developing. The bugs were especially numerous along the suture line of the follicle.

The milkweed has both horizontal and vertical surfaces of varying degree, upon which bugs can aggregate. The bugs will aggregate more readily on certain parts of the plant. "Localization of feeding sites and the ability to mate while feeding may serve to bring pairs together, especially if a peak of activity occurs during one part of the day." (Caldwell and Dingle, 1967). Linear groups may be formed when bugs meet while moving up and down the stem.

Aphis fabae will aggregate on plants because this aphid travels along major leaf veins and responds by probing when encountering a stationary individual. Aggregation is produced by aphids probing longer in certain parts of the plant and mutual visual stimulus which plays an important part in gregarious behavior (Ibbotson and Kennedy, 1951).

The milkweed bug will walk along the midrib of a leaf. Bugs will line up on the midrib, a primary feeding site, or parallel with the midrib and on the stem (i.e., parallel and linear groups).

Since there are many orientation lines on the plant (i.e., midribs, edges of leaves, stems, and petioles) it would seem that orientation lines of the plant, localized feeding sites, restriction of space, and the behavior of the bugs would be involved in the production of linear and parallel groups.

Physiological condition: Beck *et al.*, (1958) and Barrett and Chiang (1967a) report 3 intra-instar ages, pre-feeding, feeding period, and post-feeding. As the bugs grow they will go through periods of greater or lesser tendency to form groups. The tendency to group is due, in part, to the physiological changes taking place within the bugs.

Shape of bugs: The shape of the bugs is important in the formation of aggregations. The instars are generally elongate-oval, tapering towards the head. The adults are generally elongate-oblong in shape. In most aggregations, especially post-feeding groups, bugs are usually in physical contact with one another. Contact involves the antenna, legs, beak, genitals, and the body itself. The legs are often used by overlapping or touching the leg or body of adjacent bugs. Overlapping legs are commonly seen in parallel groups, whereas, the use of antenna and genitalia is commonly seen in linear groups. Body to body contact is usually found in

large compact aggregations. In loose groups the association with one bug seems sufficient in temporary grouping. In most compact aggregations bugs seem to require grouping with more than one bug.

Bugs will aggregate at feeding sites. If a milkweed seed is presented to some bugs which have been deprived of seeds for one day, the bugs will group around the seed. The bugs form a circle around the seed with their heads pointed towards the center of the seed. If there are more bugs than feeding sites available, the extra bugs will climb on top of feeding bugs so that the seed may be reached by extending their beaks between bugs. Since the head is the smallest part of the body, compact groups are occasionally formed in this circular arrangement.

In compact aggregations the bugs were sometimes in combinations of parallel and linear groups i.e., many grouped rows of bugs with the main body axis of each bug parallel to the bug lateral to it and on the same line with the axis of the bug anterior or posterior to it.

Insects or other animals that aggregate and are longer than they are wide, will form parallel groups if favorable conditions exist. Some lepidopterous larvae are examples (Olson, 1968) of this type of grouping behavior. Parallel grouping does not seem to occur, to any great extent, in round insects, unless they are oriented by an external stimulus.

Light and temperature: Changes in the behavior of the milkweed bug to humidity, light, and gravity have been reported by Barrett and Chiang (1967b). In addition, they (1967a) studied the effect of temperature on the bugs and found that, in laboratory studies, "... where a thermal heterogeneity is present, the insects were attracted to a spot warmer than the ambient temperature." They also stated, "Under field conditions, the nymphs showed a certain behavior relative to the sun." The behavior of the nymphs depends on their period of development.

The bugs are attracted to a temperature above the ambient and also to sunlight, if both sunlight and incandescent light are present.

Bugs will aggregate more readily on certain parts of the plant due, in part, to the position of the sun or radiant energy source. Since a variety of different temperatures occur on a single plant, the bugs can move to the most suitable microclimate. The change in the microclimate may be one reason for bugs not remaining in specific arrangements for prolonged periods of time.

If a temperature range occupies a small area it will cause insects to cluster as in the case of a light bulb used to produce a concentric temperature gradient. This will cause insects to form a ring in an

optimum temperature range (e.g., blowflies, Fraenkel and Gunn, 1961). Barrett and Chiang (1967a) stated, "The nymphs around the gradients were usually lined up side by side in a broken circle around the heat at somewhat equal distance from the center and at about the same temperature on the gradient. A few nymphs were situated behind these front ranks and in physical contact with them."

Compact aggregations were found to occur under 3 conditions: when a heat or light source is present, when the bugs are in a post-feeding stage (before moulting), and during the night hours. Compact groups may be involved with heat retention or control of temperature in the bugs. If the center of a temperature gradient is not too hot, the bugs will aggregate in the center of the gradient. If a temperature range occupies a large area or has homogeneity, the insects may still cluster. In the case of desert locusts, they will turn their bodies so that they are perpendicular to the sun's rays which will permit the locust to absorb more radiant energy. If conditions are too hot, the locust will climb a bush or rock and position its body parallel to the sun's rays, in this way less energy will be absorbed from the sun.

In the field, milkweed bug populations are usually of mixed ages. The changing physiological stages of the bug and the change in environment will cause the bugs to aggregate on certain parts of the plant, at certain times, and in certain ways.

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THE INVASION AND DISTRIBUTION OF THE ASIATIC CLAM (*CORBICULA MANILENSIS*) IN A SOUTHERN CALIFORNIA RESERVOIR

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ABSTRACT: *Corbicula manilensis* Philippi were probably established in El Capitan Reservoir by 1962. Relatively few live specimens, and no empty shells were observed during 1964. Empty shells were first observed during the summer of 1965 and outnumbered living specimens by 1967. Live clam populations increased from 234×10^5 individuals during the summer 1964 to a peak of $10,816 \times 10^5$ during January 1966. They declined to $6,744 \times 10^5$ during the summer 1967. These fluctuations were partially attributed to water level changes and reservoir stratification. Thermal and chemical stratification limited the depth distribution of *Corbicula* to the shallow, aerated depths during stratified periods. Their distribution extended to all depths following prolonged periods of artificial destratification. *Corbicula* densities appeared positively correlated with sediment mean particle size.

Corbicula were reported established in this hemisphere by 1938 (Ingram, 1948) from an unknown source. Filice (1958) indicated they may have been introduced accidentally to the Columbia River estuary, Washington, with seed oyster (*Ostrea gigas*) importations. However, this possibility seems remote since *C. manilensis* is a freshwater species (R. O. Fox, pers. comm., 1970). Since their introduction, they have spread rapidly through the west coast states and the Ohio River basin (Sinclair and Isom, 1963). Fox (pers. comm.) now places their distribution "in 21 states, Baja California and Sonora, Mexico."

While considered a delicacy in their native Japan, they are a nuisance organism in many local waters. They were a problem in the Coachella Valley canals, California, by 1953, (Ingram, 1959), and clogged pumps at the Tennessee Valley Authority steam plants in 1960 (Sinclair and Isom, 1963). Two to three feet of *Corbicula* bearing sediments were deposited in the Interim Canal of the South Bay Aqueduct, California, within a few years (California Dept. Water Resources, 1967). Clams greatly accelerate sedimentation by their shell deposits and by removing suspended solids from the water and depositing them in a slime that is not easily suspended (Prokopovich, 1969).

Corbicula constitute a biomass that is not readily available to higher trophic levels; only a few fish feed on *Corbicula*. No effective biological control of *Corbicula* is known, but chemical or mechanical control is possible in some cases (Sinclair, 1964; Isom, 1971). Screens may prevent adult clam move-

ments, and chlorination may control veliger larvae. These methods are expensive and more effective in closed water channels. No control is recommended for large open waters.

El Capitan Reservoir impounds the intermittently flowing San Diego River, San Diego County, California. The reservoir was completed in 1935 and filled to capacity during 1938 (Fast, 1968). It is a eutrophic and warm monomictic fluctuating reservoir. Its water source is mostly runoff, although since 1958 it has periodically stored imported Colorado River aqueduct water. *Corbicula* were not reported in El Capitan Reservoir before 1964, although they were well established by this date in other San Diego County Reservoirs. This study describes the establishment of the clam, population increase, and some factors affecting its distribution within El Capitan Reservoir.

METHODS

Benthic samples were collected with an unscreened, 15 cm square Ekman dredge along transects T-1, T-2, and T-3 (Fig. 1). Transects 1 and 2 extended perpendicular from the shore to maximum depth. Transect 3 followed the San Diego River channel from its shallowest point to the lakeward terminus of transect 2. Transect 1 is the deepest, and transects 2 and 3 have the same maximum depth. Maximum depth varied between 20 and 28 meters.

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Three samples from each 2 m depth interval were collected at each transect during a collection period. Benthic collections were made on June 1, 29, July 26, and August 31, 1964; on January 30, May 27, June 30, July 28, and September 1, 1965; on January 31 and July 15, 1966; and on August 2, 1967. The summer samples represent pre-aeration, during-aeration, and post-aeration periods. The winter collections were made following a period of normal stratification, and following a period of artificial destratification. Sample size varied as a function of water depth. Increased water levels necessitated larger sample sizes.

Benthic samples were partially washed in the field through a sieve with a 0.58 mm mesh. The sample was taken to the laboratory for preservation and examination. Samples were examined as described by Fast (1970) using Anderson's (1959) sugar flotation technique. Shell lengths were measured to the nearest 0.25 mm. Unbroken and disconnected empty shells were designated as dead clams. Most empty shells were disconnected. All living and dead clams

were counted; measurements were made of both types from selected samples.

Total population size was calculated for each collection period except July 1966. Average clam density/m² for each depth interval was multiplied by the estimated bottom area in m² for that interval. Bottom area per depth interval is calculated as the difference in lake surface area between the upper and lower limits of the depth interval. Sediment analyses, temperature measurements, oxygen determinations, and other techniques were described by Fast (1968).

RESULTS

California *Corbicula* are probably from the same genetic stock. Most previous identifications by Ingram and others call the clams *C. fluminea*. The Ohio River basin clams have characteristics of both *C. fluminea* and *C. manilensis* (Sinclair and Isom, 1963). Dr. William J. Clench identified our El Capitan clams as "*C. manilensis* Philippi, which is now widely distributed throughout much of the Ohio River system [pers. comm., 1968]."

Corbicula manilensis entered El Capitan Reservoir before 1964. They were not numerous by this date, even though several large specimens were collected (Figs. 2, 3). Only 166 live specimens and no dead specimens were observed during 1964 (Table 1). The largest 1964 specimen measured 13.7 mm. Although the total estimated number of living clams increased greatly from 1964 through 1967,

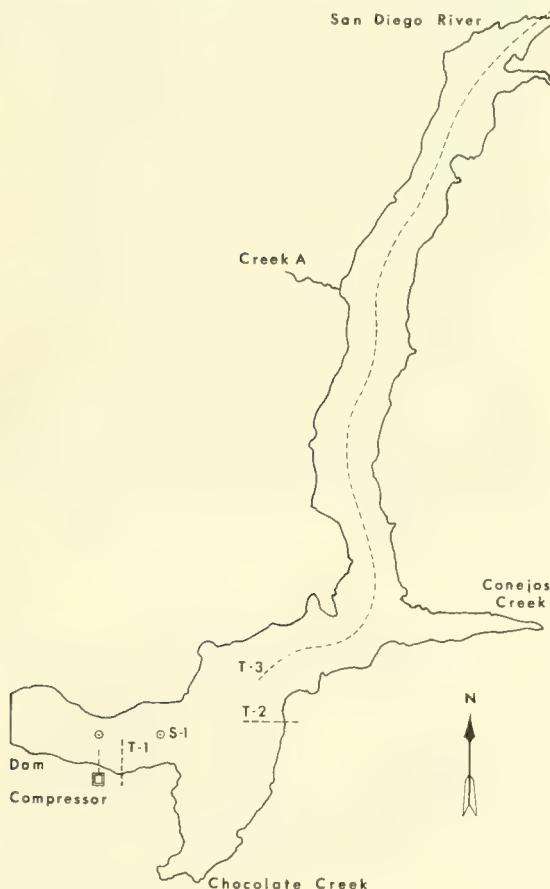


Figure 1. El Capitan Reservoir including sampling locations, compressor sites, and major tributaries.

Total Number of *Corbicula* ($\times 10^8$)

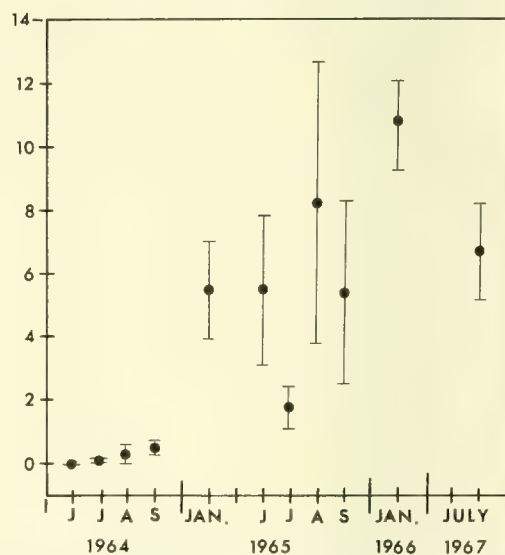


Figure 2. Total population estimates of El Capitan Reservoir *Corbicula* from June 1964 through July 1967. Total population estimates plus or minus one standard error are shown.

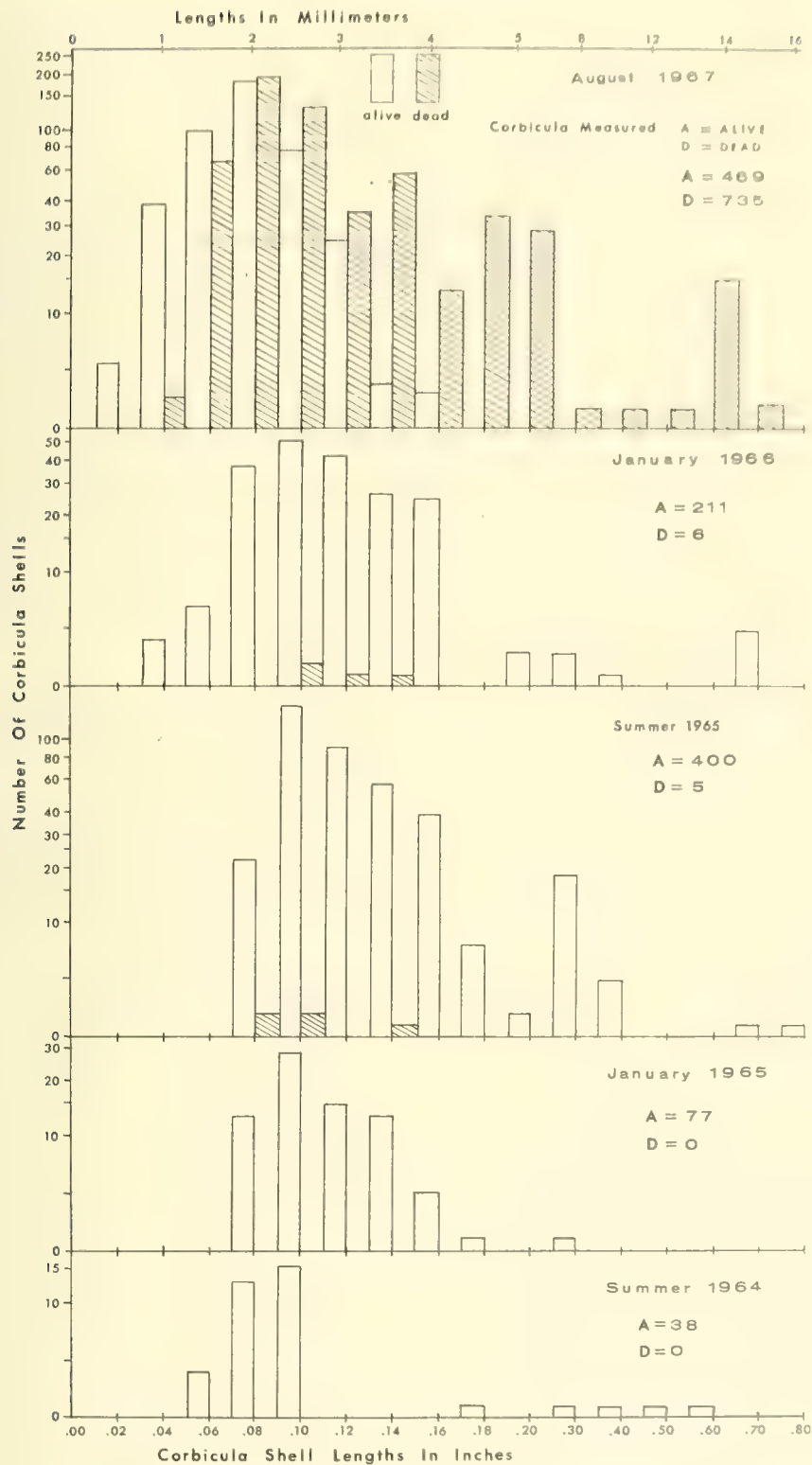


Figure 3. Length distributions of live and dead *Corbicula* during summer 1964 through August 1967

empty shells were not abundant until the summer of 1967. No empty shells were observed until summer 1965. The estimated live population ranged from an average minimum of 234×10^5 ($\pm 384 \times 10^5$) during summer 1964 to an average of $10,816 \times 10^5$ ($\pm 1,661 \times 10^5$) during January 1966. It subsequently decreased to an estimated $6,744 \times 10^5$ ($\pm 1,608 \times 10^5$) during August 1967. The July 1966 estimate is not included in Table 1 because only transect 1 was sampled.

Live *Corbicula* average shell lengths increased from 2.7 mm during summer 1964 to 3.1 mm during summer 1965 (Table 1). A 9.5 mm maximum average shell length occurred during summer 1966. Average shell lengths then decreased to a low of 1.7 mm during summer 1967. Associated with this decreased average shell length was a smaller live population and an increase in empty shells. Mortality rate apparently increased between 1965 and 1967. Sinclair and Isom (1963) also reported mass mortality of unknown causes of Tennessee *Corbicula* on three occasions.

Live *Corbicula* were restricted to the benthic area above 12 m during 1964 and mostly above 14 m

during 1965 (Fig. 4). Their depth distribution was ubiquitous during 1966, and bimodal during 1967.

El Capitan Reservoir stratified normally during 1964 and 1967 (Fig. 5). A well-developed thermocline existed by late May 1964, and an oxygen deficit began at 8 to 10 m during that summer.

The 1964 overturn occurred during November. The lake remained mixed until mid-March 1965 when it again stratified. The lake remained stratified through mid-June 1965. During this stratified period, hypolimnion oxygen concentrations approached zero. Artificial destratification by air injection began June 10, 1965. Compressed air was continuously injected until June 21. The lake was well mixed and oxygen was plentiful at all depths. Air injection was discontinued from June 21 through July 1, 1965. The temperature and oxygen profiles began to resume their pre-aeration configurations, but the bottom water was much warmer and the oxygen concentrations were much greater than before mixing. Air injection resumed July 1, 1965 and continued through October 4, 1965. The lake remained mixed without air injection from October 1965 through mid-March 1966.

TABLE 1. El Capitan Reservoir *Corbicula manilensis* total population estimates, maximum shell lengths, and average shell lengths of live clams and empty shells from summer 1964 through July 1967. El Capitan Reservoir average surface area and volume for each sample period is shown.

Sample period	Live <i>Corbicula</i>						EMPTY SHELLS			EL CAPITAN RESERVOIR		
	Average est. pop. size in 10^5 individual	Std. error 10^5	No. of Samples	Max. shell length (in mm)	Mean shell length (in mm)	No. meas.	No. observed in total samples	Max. shell length (in mm)	Mean shell length (in mm)	No. meas.	Surface area in 10^6 m ²	Volume in 10^7 m ³
Summer 1964 ¹	234	384	288	13.7	2.7	38	166	—	—	0	1.4	1.3
January 1965 ²	5,546	1,653	72	5.6	2.6	77	571	—	—	0	1.4	1.1
Summer 1965 ¹	5,249	6,220	387	19.3	3.1	400	1,106	3.81	2.8	5	1.8	1.8
January 1966 ²	10,816	1,661	102	17.0	2.8	211	1,714	3.81	3.2	6	1.9	2.0
July 1966 ³	—	—	—	15.2	9.5	43	115	3.30	2.9	4	2.2	2.5
August 1967 ²	6,744	1,608	113	3.8	1.7	462	645	19.30	4.4	735	2.3	2.7

¹Estimates from four monthly sample collections from transects 1, 2, and 3.

²Estimates from one sample collection from transects 1, 2, and 3.

³Estimate from one sample collection from transect 1 only.

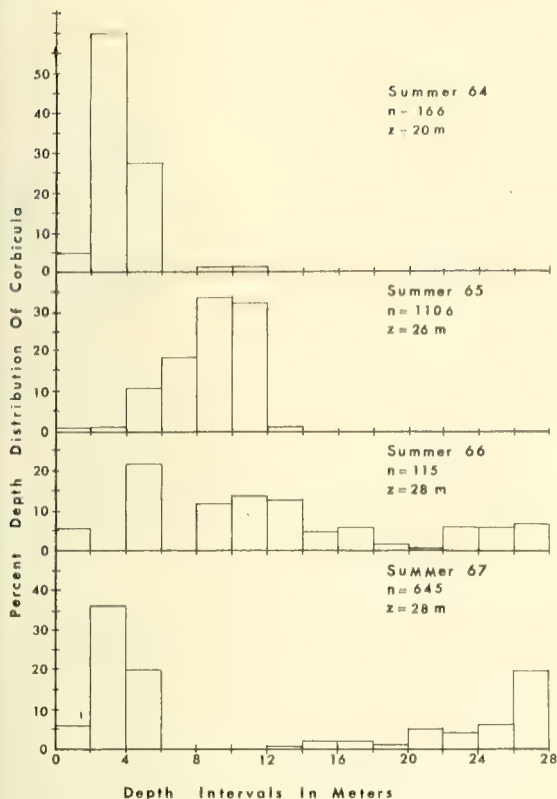


Figure 4. Depth distributions of live El Capitan *Corbicula* during the summers of 1964 through 1967. Only transect 1 was sampled during summer 1966. Maximum depth for each period is designated by (z), and (n) designates numbers.

The average clam depth distribution during summer 1965 was deeper than during 1964, but maximum depth during both periods was about the same. Destratification beginning during June 1965 did not significantly affect their maximum depth distribution during summer 1965.

The lake began to stratify during mid-March 1966. Air injection commenced March 19, 1966 and continued through October 17, 1966. The lake was well mixed during 1966 and oxygen was abundant at all depths. The lake remained mixed from October 1966 through February 1967. Clams were well distributed to all depths during the summer of 1966.

Stratification developed normally during March 1967 (Fast, 1968). Hypolimnion oxygen concentrations declined, but did not fall below 0.1 mg/l by September 1967. *Corbicula* were again more restricted to the shallower depths. Over 70% of all clams collected during August 1967 were above 6 m. The remainder were distributed from 12 m to maximum depth of 26 m. Few live clams were

found between 6 and 12 m. The reason for their absence in this zone is unknown. Most of the 1967 empty shells were collected below 6 m.

Water volume and maximum depth fluctuated markedly during the study period. Water volume fluctuated between a $1.1 \times 10^7 \text{ m}^3$ minimum to a 2.7×10^7 maximum during the study period (Table 1). Not shown are rapid drawdowns during both summers 1966 and 1967. These drawdowns followed large volume increases caused by winter and spring rains.

Corbicula concentrations were always greater at transect 2. Transect 1 had the next greatest concentrations, and transect 3 was low (Fig. 7).

DISCUSSION

The size distribution of live clams, and the absence of empty shells indicate the oldest El Capitan clams found during 1964 were 2 years old. Although the 1964 sample size is small, 2 age groups appear present with one group ranging from 4.1 mm to 13.7 mm, and the other from 0.1 mm to 2.5 mm (Fig. 3). The smaller group may be the progeny of the larger. Sinclair and Isom (1963) found that 1 year old Tennessee *Corbicula* (probably *C. manilensis*) reached sexual maturity at about 6.5 mm, and they aged a 29 mm clam at 4 years. Ingram (1959) estimated 50 mm Oregon *Corbicula* were about 7 years old.

There are indications that the population fluctuates yearly, reaching a maximum during the winter and a minimum during the summer (Fig. 2; Table 1). This pattern may be confounded by the initial population growth. This pattern is related to their reproductive cycle. Late fall and early winter reproduction would produce a maximum population density during the winter. The population would consequently decrease through natural mortality and reach a yearly minimum by the next fall. Average shell lengths demonstrate this relationship with January average lengths less than the preceding or following summer average lengths. These decreases indicate the January populations consist of younger clams and are evidence for a fall reproduction period.

El Capitan *Corbicula* were probably established by veligers from imported waters. Fish and their native water from many sources were periodically stocked in El Capitan (Fast, 1966). Colorado River water via aqueducts was periodically stored in El Capitan since 1958. *Corbicula* were reported from the Colorado River aqueduct intake of the Metropolitan Water District since 1958 (Ingram, 1959) and are well established in all San Diego County reservoirs routinely receiving this aqueduct water.

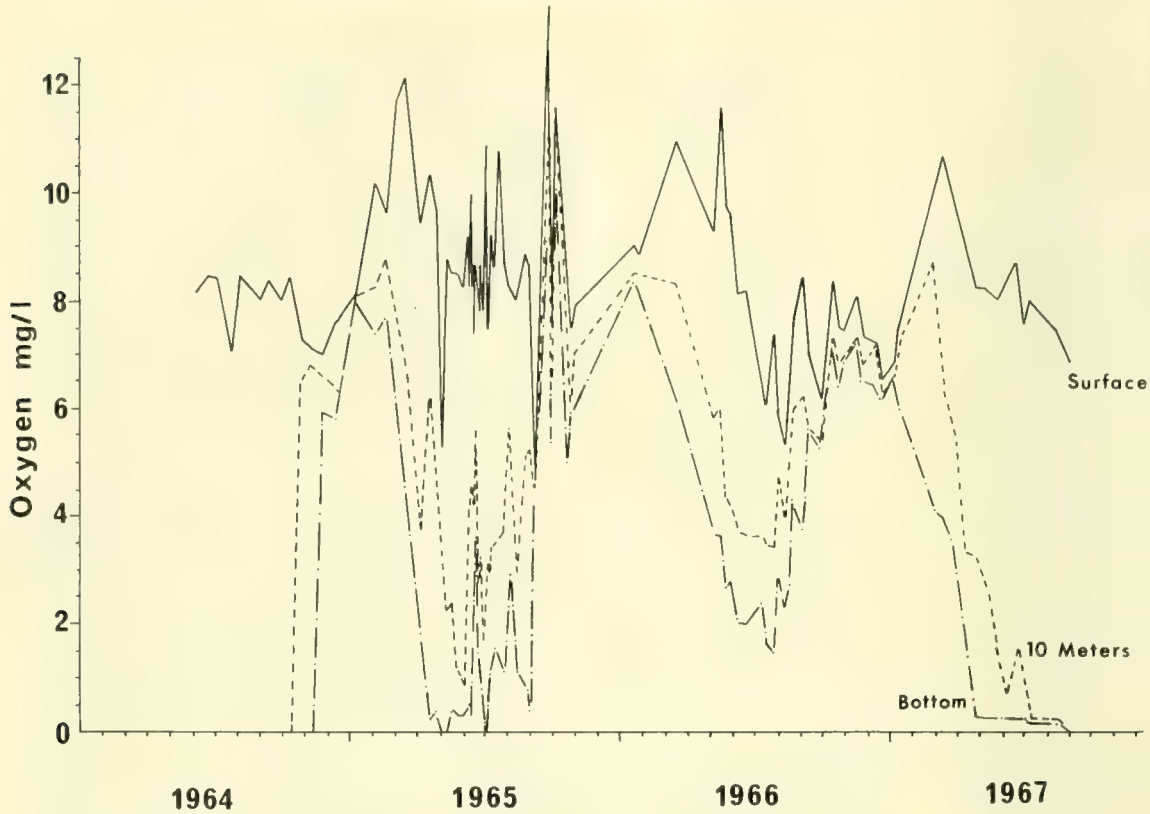


Figure 5. El Capitan oxygen concentrations at the surface, 10 m depth, and the bottom from May 1964 through September 1967.

Adult *Corbicula* are sometimes used as bait in California, but this practice is uncommon in San Diego County. Their most common natural means of dispersal are hydraulic movement of the adult clam, and passive movement of the veliger larval stage. Diverted or imported water within or between drainage systems greatly accelerates dispersal.

Colorado River water was diverted into El Capitan Reservoir during October through January in 1958, 1962, and 1963. Any of these importations could have introduced veligers. The California Department of Water Resources (1967) observed veliger larvae in the Interim Canal of the South Bay Aqueduct from October 29 through January 20. They sampled from October 22, 1964 through May 6, 1965. Their adult clams had characteristics of both *C. manilensis* and *C. fluminea*.

Physical-chemical stratification and sediment composition are probably the two most important factors affecting *Corbicula* distribution within a reservoir. Hypolimnetic stagnation during 1964 undoubtedly restricted clams to shallow depths. Still, some live clams were collected below the

oxygen deficit. Although *Corbicula* have a high tolerance to low oxygen tension (Sinclair and Isom, 1963) prolonged exposure to 0.0 mg/l oxygen is fatal. Clams collected between 8 and 12 m may have been transients and move up and down the slope to avoid prolonged exposure to the stagnant water. Another possibility is that they reside in this depth zone. Internal seiches of the thermocline could have alternately bathed them with stagnant and aerated water, and although the oxygen deficit was relatively constant in the middle of the lake, fluctuations in its depth may have occurred at the lake bottom-thermocline juncture.

Corbicula maximum depth distributions were about the same during the summers 1964 and 1965 even though the reservoir was destratified after mid-June 1965 (Figs. 4, 5). This indicated their depth distribution was largely determined before mid-June and the adult clams did not actively migrate after this period.

Clams were abundant at all depths during 1966. I attribute this dispersal to early air injection, since strong stratification was not allowed to develop

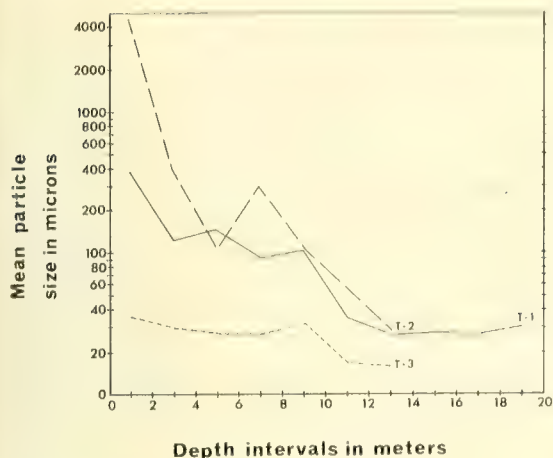


Figure 6. Mean particle diameter of El Capitan sediments collected from transects 1, 2, and 3.

anytime during 1966. The clams were still most abundant between 4 and 14 m. This was probably a result of a time lag in their dispersal, rather than a preference for the sedimental conditions, since they were scarce in this interval during 1967. However, sediment conditions were quite varied at T-1. The shallow depths were predominately sand and gravel (Fig. 6), whereas, the deeper areas were predominately fine colloidal matter with a high organic content (Table 2).

Most *Corbicula* were again restricted to shallow depths by stratification during 1967, but about 30% were found within the hypolimnion. Hypolimnetic conditions during 1967 were not as severe as during 1964, but oxygen concentrations approached zero by September 1967. While some *Corbicula* tolerated the low hypolimnion oxygen concentrations and associated stagnation, many may have perished after stratification developed. This could have contributed to the great population decrease between January 1966 and August 1967.

The effect of reservoir volume changes on *Corbicula* are unknown. Increased volume increases the total bottom area available to the clams. This new area is predominately sand and gravel covered by sparse terrestrial vegetation. Decreased water volumes concentrate the clams and creates less desirable conditions. The rapid drawdowns during 1966 and 1967 may also have contributed to the high mortalities, but Sinclair and Isom (1963) do not recommend water level change for controlling *Corbicula*.

Several factors undoubtedly influenced the clam spatial distribution between transects. Foremost among these considerations are: (1) sediment par-

ticle size and composition, (2) current patterns, and (3) location of initial introduction.

Transects 1 and 2 have similar mean particle size distributions with depth (Fig. 6). However, transect 2 has much coarser sediments in the shallow depth. There appears to be a direct relationship between the mean particle size of the shallow water sediment at each transect and the clam densities. Transect 1 is mostly fine colloidal material at all depths and always had very low *Corbicula* densities. San Francisco Bay *Corbicula* prefer sandy substrates to mud (Filice, 1958). Other authors observed similar preferences by *Corbicula* (Villadolid and Del Rosario, 1930; Cahn, 1951).

Surface water currents usually flow from the dam towards the upper end of the reservoir (Fig. 1). Veliger positive phototaxis would result in their transport from transect 1 towards transects 2 and 3. By this rationale, transect 3 receives the greatest concentration of young *Corbicula*, transect 2 the next greatest and transect 1 the least. Such a concentration gradient among mature clams was not observed. The hypothetical larval distribution may be modified by active selection for sediment composition. If the veligers select for larger sediment particle size, transect 2 may be the most desirable. Most of the larvae would reject transect 3 and delay settling until they were carried by the currents to transect 2 or 1. The fine sediments of transect 3 could also cause high mortality during the maturation of those clams that settle there.

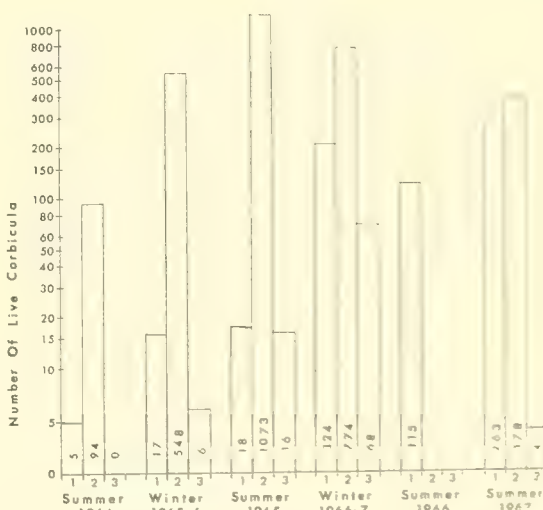


Figure 7. Numbers of El Capitan *Corbicula* collected at transects 1, 2, and 3 from summer 1964 through summer 1967. Transects 2 and 3 were not sampled during summer 1966.

TABLE 2. Total solids, chemical oxygen demand, and nitrogen content of El Capitan Reservoir bottom sediments during August and November 1964 at Transect 1.

Depth (meters)	AUGUST 1964			NOVEMBER 1964		
	% total solids	C.O.D. (mg/gm)	% N ₂	% total solids	C.O.D. (mg/gm)	% N ₂
0.5	63.6	43.27	0.099	79.0	4.49	0.014
5.0	67.6	25.12	0.082	67.0	49.78	0.130
10.0	22.2	105.48	0.390	46.0	65.70	0.186
15.0	25.8	85.25	0.302	24.2	101.70	0.352
20.0	20.0	125.05	0.468	23.2	122.21	0.457

ACKNOWLEDGMENTS

Many people contributed to this study and their contributions are appreciated. William J. Clench, Museum of Comparative Zoology, Harvard University, identified the clams. Robert Doyle measured all *Corbicula* lengths, made many of the sample counts, and devoted much time to this study. R. O. Fox, California Academy of Science, reviewed the manuscript.

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TWO BOPYRIDS (ISOPODA) FROM NEW GUINEA

CHARLES G. DANFORTH¹

ABSTRACT: The female *Parathelges weberi* has been previously described but the male, host, and locale were unknown. These data are here provided and a new species of *Pseudione* is described from the same area

Four parasitized crabs were obtained from the collection of the "Alpha Helix" Expedition to New Guinea. From a study of these forms, it was determined that there were 2 epicarid isopod genera — one parasite represented a new species of *Pseudione* (a branchial bopyrid); while the other was the first record for the male, the host, and the area for *Parathelges weberi* (an abdominal bopyrid).

Parathelges weberi Nierstrasz
and Brender à Brandis, 1923.

Figure 1A

Host: Female of *Calcinus laevimanus* (Randall).
Site: Lagoon, 22 miles north of Maiwara, Northeast New Guinea, at 0-2 feet, on broken coral bottom.
Date: 21 September 1969. **Collector:** K. Kirk, I. Richards, and E. Ball. The host and site given here are the first record for the species.

Description: Female. Essentially the same description as that given by Nierstrasz and Brender à Brandis (1923). Located on the dorsal abdomen of the host, with the head of the parasite directed towards the posterior of the host, and the dorsum of the bopyrid against the host. The measurements of the holotype were 9 mm by 3.25 mm, whereas the new specimen measured 6 mm by 2.5 mm. No hyperparasites were found in the marsupium of the "Alpha Helix" form, whereas, a *Duplorbis smithi* was reported from the brood chamber of the "Siboga" specimen (Nierstrasz and Brender à Brandis, 1923).

Male. 2.5 mm greatest length, 1.0 mm greatest width. Antennae I short, 2-3 articles. Antennae II long, 5 articles, with many flagellum subdivisions. Eyes obvious, though small. Cephalon definitely separated from thoracomere I. Pereopods in a group of 3 pairs, then a gap, followed by the posterior 4 pairs. No mid-ventral tubercles. Scattered, weak, dorsal pigment spots. Lateral portions of thoracomeres non-contiguous, with the largest gap between III and IV. All thoracomeres the same length. Pleon completely fused, with a clear "envelope" peripherally. Pleon length about equal to

total width of 3 thoracomeres. No pleopods. Slight mid-ventral pigment spots.

Remarks: Whitelegge (1897) described a new bopyrid species from Funafuti (Ellice Islands) which he named *Athelges aniculi*. Bonnier (1900) changed this to *Parathelges aniculi* (Whitelegge 1897), on the basis of the lack of sudden size diminution between the pereon and the pleon, such as is found in *Athelges* (accepted spelling). Nierstrasz and Brender à Brandis (1923) recognized this generic difference, and erected the new species *P. weberi* for a specimen in the "Siboga" collection which showed neither host nor locale. These authors indicated that *P. weberi* was similar to *P. aniculi*, but gave adequate points of difference to justify the former species.

There are 2 other species of *Parathelges* — *P. racovitzae* Codreanu (1940) and *P. whiteleggei* Nierstrasz and Brender à Brandis (1931) — plus several related genera such as *Anathelges* Bonnier (1900), *Athelges* Hesse (1861), and *Metathelges* Nierstrasz and Brender à Brandis (1923). Previous works in New Guinea by authors such as Nobili (1905) and Weber (1892), did not mention any form which could have been *Parathelges weberi*.

Despite the wide European and Pacific distribution of the "Athelges" types, there are apparently none in North America (Danforth, 1970).

The female and male described herein have been deposited in the Allan Hancock Foundation Collection, University of Southern California.

***Pseudione novaeguineensis*, new species**

Figure 1B-G

Pseudione Kossman 1881.

Host: *Clibanarius* sp., aff. *longitarsus* (De Haan).
Site: On mangrove roots, near Maiwara, New Guinea, lat. 5°44' S, long. 145°43.7' E. **Date:** 26 October 1969. **Collector:** E. Ball.

Description: Female. Length 3.5 mm, width 2.0 mm. From right gill chamber of host: head of bopyrid directed downward and to rear. Marsupium

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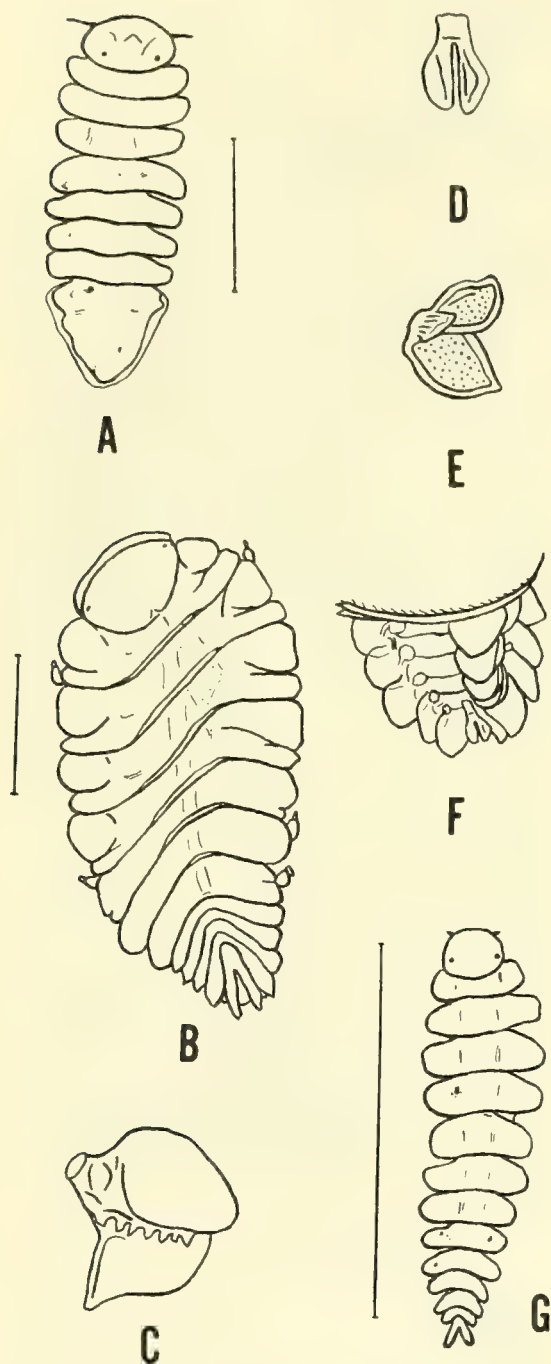


Figure 1. A, *Parathelges weberi*, dorsal aspect of male, scale equals 1 mm. B-G, *Pseudione novaeguineensis*, new species: B, dorsal aspect of female, scale equals 1 mm; C, inner aspect of oostegite I; D, ventral aspect of uropoda of female; E, right pleopod I of female, exopodite is the larger; F, ventral portion of female pleon, right pleopods removed; G, dorsal aspect of male, scale equals 1 mm.

towards host branchiostegite. Cephalon slightly bilobed posteriorly. Eyes present, but tiny. Frontal margin of cephalon upturned to form a "velum." Head sunken into thorax.

Thorax of 7 thoracomeres, I-IV with anterolateral and post-lateral plates. Coxal plates very poorly indicated on first 4 right segments. Seven pairs of small, well-formed pereopods. No swelling on basal articles of the legs. Five pairs of oostegites, barely meeting over the marsupium. Oostegite I with pronounced teeth on inner aspect. Dorsum quite concave, without tubercles. Two epicaridea larvae in the marsupium.

Abdomen of 5 pleomeres, tapering rapidly posteriorly. Pleomeres strongly arched anteromedially, clearly demarcated, with pleural ends non-contiguous. Segment V so arched as to appear bifurcated. Five pairs biramous pleopods, each ramus leaflike and subequal. One pair uniramous uropods on telson, which appears to be fused to mid-ventral surface of pleomere V.

Male. Length 1.1 mm, width 0.3 mm. Body fusiform. Head sunken into, but not fused with, thoracomere I. Eyes obvious. Antennae I and II short (2-3 articles), barely evident in dorsal view.

Thorax of 7 thoracomeres, having widely separated terminations. Seven pairs of large pereopods. No mid-ventral tubercles. Scattered pigment spots dorsally.

Abdomen of 6 pleomeres, sixth sharply arched. Lateral plates widely separated. No pleopods, although occasional swellings present and unpaired.

The female holotype and the male allotype are deposited in the Allan Hancock Foundation Collection, no. 694 and 694a, respectively.

Remarks: Two other crabs of the same description, and parasitized by the same bopyrid species, were found at the collecting site. However, none was as clearly segmented as were the selected holotype and allotype. Both sexes of the host were parasitized.

Descriptions and identifications of *Pseudione* in the literature leave considerable question as to uniformity of critical features. As summarized by Danforth (1970), Sars (1899) indicated that *Palaegyge hoylii* was equivalent to *Pseudione affinis*; Barnard (1920) said that *Palaegyge* and *Pseudione* could be best separated by the warts on the female pleopods (which are variable); Calman (1898) apparently felt that *Palaegyge borrei* was essentially the same as *Pseudione giardi*; Nierstrasz and Brender à Brandis (1929) felt that *Palaegyge* might be *Probopyrus*, and Van Name (1936) indicated that if this were so, *Probopyrus* had priority; Nierstrasz and Brender à Brandis (1931) substituted *Pseudione* for the genus *Cryptione*; Stock (1960) felt that

Pleurocrypta porcellanae should be *Pseudione convergens*, but this was contested by Bourdon (1965); etc.

With approximately 60 species of *Pseudione* so far described, identification of a new form is quite difficult, and requires a survey of the original papers. The only original description not obtained for comparative study was that by Rodriguez y Femenias (1886), in which Kossmann apparently described *Palaegyge fraisei* as a footnote on page 3. This form was then called *Pleurocrypta balearica* by Giard and Bonnier (1887), and later *Pseudione fraisei* by Stebbing (1893). In view of the complexity and confusion surrounding the genus, Nierstrasz and Brender à Brandis (1923) attempted to sort *Pseudione* into 3 groups: (a) having no abdominal plates, (b) having distinct abdominal plates plus unseparated coxal plates, and (c) having distinct abdominal plates plus separated coxal plates. However, there are many intermediate forms, which necessitates checking the original works.

Pseudione novaeguineensis most nearly approaches *P. calcinii* Shiino (1958), and *P. diogeni* Popov (1924). It is very close to the first, but differs from the female in the sharpness of the pleomere plates, in the greater width and shorter length of the uropoda, in the greater breadth of the pleopoda, in the presence of teeth on the inner aspect of oostegite I, in the double flexion of the body axis, in the more narrow body width, and as to the host. There was no male reported for *P. calcinii*.

Although the females of *P. diogeni* and *P. novaeguineensis* are similar, differing only regarding oostegite I, the mid-dorsal pleon fusion, and the separation of pleopod rami, the males of the 2 species are drastically different. [It is interesting to note that Caroli (1948) felt that *P. diogeni* might be the same as *Gyge arcassonensis*]. There are also points of similarity with the female of *P. giardi* Calman (1898), and with the male of *P. tattersalli* Nierstrasz and Brender à Brandis (1923), but in each case the descriptions of the other sex do not coincide.

As can be concluded from the foregoing the taxonomy of bopyrids as a whole, and of *Pseudione* specifically, should be critically reviewed.

ACKNOWLEDGMENTS

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A NEW INTRANASAL CHIGGER OF THE SUBGENUS *CRYPTICULA*,
GENUS *MICROTROMBICULA* (ACARINA: TROMBICULIDAE) FROM TEXAS

RICHARD B. LOOMIS AND JAMES P. WEBB, JR.¹

ABSTRACT: A new species of *Microtrombicula* (*Crypticula*) is based on intranasal larvae from *Peromyscus pectoralis* trapped near Del Rio, Val Verde Co., Texas.

Webb and Loomis (1970) reported nine intranasal species which belong to the subgenus *Crypticula* Webb and Loomis of the genus *Microtrombicula*: five from North America and four from Korea. *Microtrombicula diabolus* Webb and Loomis (1970) was taken from two *Peromyscus difficilis nasutus* (rock mouse) trapped near Del Rio, Texas and attempts to obtain additional larvae from near the type locality (now under water of the Amistad Reservoir) yielded a second new species which is described below. Studies upon which this paper is based were supported by the U.S. Public Health Service Research Grant AI-03407 from the National Institute of Allergy and Infectious Diseases.

Microtrombicula welbourni, new species

Figure 1

Types. — Larvae: Holotype and 11 paratypes from the nasal passages of 2 *Peromyscus pectoralis laceianus* (white-ankled mouse) taken 10 mi N, 8 mi W Del Rio, 1000 ft, Val Verde Co., Texas, 28 July 1970, by W. C. Welbourn, Jr., R. B. Loomis, and R. C. Stephens, original numbers WCW700728-15 (holotype and 10 paratypes) and WCW700728-

14 (1). The holotype and one paratype will be deposited in the collection of the Rocky Mountain Laboratory, Hamilton, Montana, and available paratypes will be sent to appropriate institutions.

Diagnosis. — Larva differing from all other members of the subgenus *Crypticula* in having 3-5 setae on coxa III (*M. ornata* bisetose, other species unisetose), and from *M. diabolus* in possessing eyes, nude galeala, and dorsal knob on cheliceral blade.

Description of holotype (all measurements in microns, with means and ranges of all 12 types in parentheses, unless otherwise indicated). — Body engorged, 580 by 410; color in life, pale yellow; eyes 2/2, anterior larger, ocular plate indistinct.

Dorsal setae 2-6-6-6-6 + 14, total 40; measurements of humeral seta 43, anterior dorsal seta 29, posterior dorsal seta 27.

Ventral setae 2-2 (sternals) + 48, total 52; measurements of anterior sternal seta 29, anterior ventral seta 28, posterior ventral seta 29.

Scutum: Subpentagonal: with large puncta in reticulate pattern; sensilla flagelliform with 3-5

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Figure 1. *Microtrombicula (Crypticula) welbourni*, new species. A. Scutum and eyes. B. Dorsal aspect of gnathosoma. C. Ventral aspect of palpotibia and tarsus. D. Leg I, genu, tibia, and tarsus, showing nude setae (measurements in microns) and bases of branched setae. E. Leg II, as above. F. Leg III, as above. G. Body setae: 1 ST, first sternal, H. humeral, PD. posterior dorsal, H. Coxa III.

distal branches and several short proximal barbs.

Scutal measurements: AW 36 (34, 32-36), PW 50 (48.5, 47-50), SB 21 (20, 19-22), ASB 21 (22, 21-23), PSB 25 (26, 25-28), AP 28 (31, 28-33), AM 28 (29, 25-33), AL 24 (21, 19-24; 11), PL 29 (30, 28-32), S 60 (57, 53-60; 8).

Gnathosoma: Cheliceral blade with small tri-

cuspid cap and dorsal knob; cheliceral base and capitular sternum lightly punctate. Galeala nude. Palpal setae B/B/NbB; palpotarsus with 1 nude and 5 branched setae, and tarsala 9; palpotibial claw bifurcate, axial prong slightly curved. Leg I, coxa unisetose, 2 genualae and microgenualae, 2 tibialae and microtibialae, tarsala 24 (24, 22-26), distal microtarsala, subterminala, parasubterminala, and pretarsala; leg II, coxa unisetose, 2 tibialae, tarsala 19 (19, 17-20) and proximal microtarsala; leg III coxa with 3 and 4 (3 to 5) branched setae, genualae tibialae, and 1 nude mastitarsala (39).

Leg measurements: I 214 (209, 192-226), II 205 (190, 174-205), III 236 (225, 211-239), total 655 (625, 577-655).

Remarks. — The cheliceral blade has a prominent knob characteristic of the four Korean species described by Ah (1964), but not conspicuous among the American *Crypticula*.

The geographic proximity of *M. welbourni* to *M. diabola* (type localities less than 3 miles apart), may indicate an ecological relationship similar to the two sympatric species *Microtrombicula nasalis* and *M. wrenni* Loomis, recovered from the same individuals of several cricetid rodent species in Joshua Tree National Monument, California (Loomis, 1963).

This new species is named after Mr. W. C. Welbourn, Jr. of California State College, Long Beach in recognition of his numerous contributions to the studies of trombiculid mites.

Specimens examined (17). — Type series (12) plus 5 larval skins (WCW700728-15).

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COVER: A mass stranding of 28 Pacific pilot whales, *Globicephala macrorhyncha* Gray, at Pyramid Cove, San Clemente Island, California. The stranding occurred on January 8, 1971 and included 6 males, 21 females, and 1 of undetermined sex. *Globicephala* appears to be subject to mass stranding more frequently than any other cetaceans. Climatic and biological factors (high tide, no surf, slight wind, sloping beach with steep dropoff, and spawning squid) may have contributed to the stranding.

Photograph by Donald B. Bright

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Erratum: The date of publication for Vol. 70(2) should be corrected to March 1, 1972.

TAXONOMIC STUDIES AND NOTES ON
SOME HONDURAN AMPHIBIANS AND REPTILES

JOHN R. MEYER¹ and LARRY DAVID WILSON²

ABSTRACT: Fourteen species of amphibians and reptiles occurring in Honduras are discussed. *Anolis humilis*, *Anolis crassulus*, *Anolis laevis*, *Ninia atrata*, *Rhadinaea kinkelini*, *Sibon anthracops*, and *Thamnophis cyrtopsis* are recorded from the country for the first time. *Eleutherodactylus merendonensis*, previously considered a synonym of *Eleutherodactylus rugulosus*, is resurrected. *Anolis humilis* and *Anolis uniformis* are raised to specific rank from their former subspecific status. *Anolis intermedius* and *Anolis nannodes* are synonymized with *Anolis laevis*, and *Anolis heteropholidotus* is relegated to the synonymy of *Anolis sminthus*. New distributional and taxonomic data are also given for *Anolis anisolepis*, *Anolis bouvierii*, *Anolis cobanensis*, *Sphaerodactylus dunni*, *Bothrops bicolor*, *Dryadophis dorsalis*, *Lampropeltis triangulum*, and *Sibon carri*.

For the past seven years we have been studying the herpetofauna of the Republic of Honduras, and in the course of this research have encountered specimens that have necessitated taxonomic revision or have contributed to the clarification of the status of little-known forms. Accounts of the distribution, relationships, and ecology of all of the Honduran amphibians and reptiles will be treated in a separate paper.

Eleutherodactylus merendonensis Schmidt

This species was described by Schmidt (1933) on the basis of a single specimen from an elevation of 150 m in Santa Ana Canyon, Departamento de Cortés, Honduras. In August 1968 we collected 13 specimens (LACM 48010-22) of *Eleutherodactylus*, which later proved to be referable to *merendonensis*, from the approximate type locality of the species. All 13 individuals were found at night in the open on boulders, logs, and rock ledges along the Río Santa Ana at an elevation of 200 m; this locality is immediately below a small reservoir about 3 km west of San Pedro Sula.

Lynch (1965), in a paper dealing with the *rugulosus* group of *Eleutherodactylus* in northern Central America, placed *merendonensis* in the synonymy of *E. rugulosus*. In synonymizing the two species, Lynch stated that "the difference between *merendonensis* and *rugulosus rugulosus* are [sic] size or due to size. The type of *merendonensis* is a very large specimen (80 mm) thus paralleling *E. r. natator* in size. Direct comparison of the type and specimens of *E. r. rugulosus* from Mexico reveals that the two are identical."

We have examined the holotype (FMNH 4672) of *merendonensis*, and find it and the 13 additional specimens to be distinguishable from *rugulosus* in the following features: 1) web between toes IV and V incised no deeper than distal tubercle of toe V in *merendonensis* (web virtually absent between toes IV and V in *rugulosus*), and 2) inner tarsal fold large and flap-like in *merendonensis* (inner tarsal fold ridge-like, not free at edge in *rugulosus*). In addition, *merendonensis* appears to be a larger and much stockier species than *rugulosus*, with the snout-vent length of adult *merendonensis* being 75-85 mm, whereas the maximum snout-vent length of adult *rugulosus* from Honduras is about 60 mm. The two species are sympatric (although apparently not in the sense of utilizing the same microhabitat), as we found *rugulosus* to be common along the Río Santa Ana below the *merendonensis* locality at an elevation of 100 m, and also in small seeps on the hillside above the *merendonensis* locality.

Although the relationships of *merendonensis* are apparently with the *rugulosus* group of *Eleutherodactylus*, the species resembles *E. punctariolus* from lower Central America more closely than it does *rugulosus*. Both *merendonensis* and *punctariolus* are large, stocky frogs, but *punctariolus* differs from *merendonensis* in having considerably more webbing on the feet (toes about 1/2 to 2/3 webbed in *punctariolus*, as opposed to about 1/3 webbed in *merendonensis*).

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Anolis humilis Peters

Stuart (1948) proposed recognition of a subspecific relationship among populations of three small anoles previously considered as distinct species, *Anolis humilis*, *A. quagglus*, and *A. uniformis*. *Anolis humilis* was described by Peters (1863) from Veragua, Panamá, *A. quagglus* by Cope (1885) from Río San Juan, Nicaragua, and *A. uniformis* by Cope (1885) from Yucatán and Guatemala. According to Stuart's (1948) arrangement, *A. h. uniformis* ranges from Veracruz, México to Honduras, where it presumably intergrades with *A. h. quagglus*, which in turn ranges from Honduras to Costa Rica, where it intergrades with *A. h. humilis*. Taylor (1954a) described a fourth subspecies, *A. h. marsupialis*, from southeastern Costa Rica.

In relegating *humilis*, *quagglus*, and *uniformis* to subspecific status, Stuart (1948) stated that *uniformis* differs from the other two races in having larger ventrals (35-45 between levels of axilla and groin in *uniformis*, more than 50 in *quagglus* and *humilis*), and in having a brilliant purple spot on the dewlap (no spot present in *quagglus* or *humilis*). Stuart stated further that he felt the lack of specimens of *humilis* (*sensu lato*) from between Guatemala and Nicaragua was due to insufficient collecting in deep forest, and that future collecting in Honduras would reveal its presence there.

We have collected throughout most of Honduras and examined all major collections from the region, but we have encountered only one specimen of *humilis* from the country (TCWC 23628, from ca. 40 km E of Catacamas, Departamento de Olancho, located about 30 km from the Nicaraguan border). The nearest locality record to the northwest is 25 km SSW Puerto Barrios, Departamento de Izabal, Guatemala (TCWC 23744), about 350 km from the Honduran locality. Examination of specimens of the *humilis* complex from throughout its range has caused us to question the advisability of following Stuart (1948) in synonymizing *uniformis* with *humilis* and *quagglus*. We propose that the two subspecies, *Anolis humilis humilis* and *Anolis humilis uniformis* be raised to specific status, with *Anolis quagglus* retained as a junior synonym of *humilis*.

In our opinion, additional collecting in Honduras will not appreciably extend the ranges of *A. humilis* and *A. uniformis* towards one another. In Honduras the ecological roles of these species, both ground dwelling or low vegetation inhabitants of the deep forest, appear to be filled by a close relative of the two, *Anolis tropidonotus*. *Anolis tropidonotus*, which is absent from most of the range of *humilis* and appears to be ecologically separated from *uni-*

formis, is the most common anole in the deep forests of Honduras. Stuart (1955) stated that *tropidonotus* is an inhabitant of savanna and dry forest in Guatemala, whereas *uniformis* is restricted to the taller, more mesic forests in that country. In occupying the mesic forests in Honduras, it may be that *tropidonotus* prevents the spread of *humilis* and *uniformis* towards one another.

Separation of the ranges of *humilis* and *uniformis* is not in itself sufficient evidence for considering the two as distinct species, and accordingly we undertook an examination of morphological features of the various populations. We examined 51 specimens of *uniformis* and 137 specimens of *humilis* from throughout their ranges, and failed to find any feature of scalation by which the two species can be consistently separated, including the supposed difference in ventrals reported by Stuart (1948). There is, however, a constant difference in the male dewlap between the populations occurring northwestward of Honduras (*uniformis*) and those found from Honduras southward (*humilis*). This difference is not merely the presence versus the absence of a spot on the dewlap (Stuart, 1948), but rather the dewlap in *uniformis* consists of a bright red ground color with a more or less anterior blue to purple spot, whereas in *humilis* the ground color is reddish-orange with a bright yellow border, with the scales on the dewlap darkly pigmented so as to suggest obliquely transverse black stripes.

Taylor (1954a) recorded *Anolis humilis uniformis* from Costa Rica and noted that the dewlap color and pattern was as described above for *uniformis*. Four specimens were reported by Taylor, all from Tenorio, Las Cañas, Providencia de Guanacaste, and a detailed description of one of these (KU 40893) was given. In examining this collection, we find that this number is allocated to the holotype of *Anolis humilis marsupialis*, and the 4 specimens of *A. h. uniformis* mentioned by Taylor actually bear the numbers KU 40922-25. Of this series, only one (KU 40925) is a male and examination of this specimen shows that the dewlap is typical of that of *humilis*, described above. In our opinion these 4 specimens (KU 40922-25) represent *Anolis humilis*, and Taylor was in error in recording *A. uniformis* from Costa Rica.

Anolis laevis Wiegmann

The name *Anolis laevis* has previously been applied to a population of medium-sized anoles found in southern México and western Guatemala, which according to Stuart (1948) is part of a series of closely related species also including *A. nannodes*, *A. dunni*, and *A. intermedius*. In Stuart's arrange-

ment, the range of *dunni* is from Michoacán to Guerrero, México, *laevis* from central Veracruz, México to western Guatemala, *nannodes* from western to central Guatemala, and *intermedius* from northwestern Costa Rica to eastern Panamá. We have not examined any specimens of *A. dunni*, and this species is excluded from the following discussion.

Anolis laevis was described by Wiegmann (1834) from "México," and the type locality was subsequently restricted to Jalapa, Veracruz (Smith and Taylor, 1950). *Anolis intermedius* was described by Peters (1863) from Veragua, Panamá. *Anolis nannodes* was described by Cope (1864) from Cobán, Alta Verapaz, Guatemala; Arriba, Costa Rica; and Jalapa, México, and was subsequently restricted to Cobán by Stuart (1948).

Dunn (1930) stated that he had compared the types of *nannodes* and *intermedius* and found them to be identical. Stuart (1948) stated that "in describing *nannodes*, Cope unquestionably confused 3 species *intermedius*, *laevis*, *nannodes*," but Stuart presented no data to indicate why he considered the three species to be distinct. In a subsequent paper, Stuart (1955) indicated that *nannodes* and *laevis* could be separated on the basis of the number of dorsal scales between the axilla and groin levels (> 60 in *nannodes*, < 60 in *laevis*); he also indicated that the 3 species differed in head scalation (slightly keeled or rugose in *laevis*, less so in *nannodes*, and smooth in *intermedius*).

In 1968 we collected 2 anoles (LACM 47291-92) obviously belonging to the *laevis* group, at La Esperanza, Departamento de Intibucá. These specimens and an additional one (KU 103239) from Cerro Uyuca, Departamento de Francisco Morazán, represent the only records for this group between central Guatemala and northwestern Costa Rica.

We have failed to find a difference in the examination of over 70 specimens of the three nominal species (*intermedius*, *laevis*, *nannodes*) from throughout the range. The supposed difference in number of dorsal scales between *laevis* and *nannodes* does not show any consistent pattern, nor is there any consistent difference in dorsal head scalation among the three. Examination of several other features of scalation shows that there is considerable overlap in various populations and indicates a lack of any clear clinal variation. Furthermore, in all three nominal populations, the males have a small, white dewlap, a character that is probably of considerable evolutionary significance. In view of the apparent lack of difference in scalation and the uniformity of dewlap coloration in this group of anoles, we propose that *Anolis intermedius* and *A. nannodes* be considered subjective junior synonyms

of *Anolis laevis*. *Anolis laevis* at present appears to be restricted to intermediate elevations of both versants from southern México to western Panamá.

Anolis sminthus Dunn and Emlen

This anole was collected by us 12 km SW San Juancito, Departamento de Francisco Morazán (LACM 47676-78, LSUMZ 21415-16), 3 km NE La Esperanza, Departamento de Intibucá (LACM 47682), and 20 km E Nueva Ocotepeque, Departamento de Ocotepeque (LACM 47679-81). In the original description, Dunn and Emlen (1932) stated that *A. sminthus* is related to *A. alba* and *A. concolor*. In our opinion this was an erroneous association, and *A. sminthus* should be included in the group also including *A. crassulus*, *A. haguei*, and *A. anisolepis* as suggested by Stuart (1955) and Smith, Burley, and Frits (1968). *Anolis crassulus* was described by Cope (1864) from central Guatemala, *A. sminthus* by Dunn and Emlen (1932) from San Juancito, 2100 m, Francisco Morazán, Honduras, *A. haguei* by Stuart (1942) from 2 km S Finca Chichén, Alta Verapaz, Guatemala, and *A. anisolepis* by Smith, et al., (1968) from 17 km SE San Cristóbal de Las Casas, Chiapas México.

In 1968 we secured a series of what we consider to be *Anolis crassulus*, in sympatry with *A. sminthus* 3 km NE La Esperanza, Departamento de Intibucá, and there is no problem in separating this series of *crassulus* from all known specimens of *sminthus*. *Anolis sminthus* may be characterized as follows: males with brick red to scarlet dewlap with white to cream scales in life; dorsal pattern of a broad dark brown stripe (δ and η), a narrow white mid-dorsal stripe (η only), or a series of faint paravertebral inverted V's (δ and η); tail rounded to oval in cross-section, scales of the dorsal caudal row of flattened aspect; mid-ventral scales smooth to faintly keeled, 34 to 42 (η) and 41 to 46 (δ) between axilla and groin. Honduran *crassulus* may be characterized as follows: males with orange dewlap with yellow scales in life; dorsal pattern a series of distinct, inverted paravertebral W's, bordered below by a white postocular stripe (δ and η); tail laterally compressed in cross-section (strongly so in δ), the scales of the dorsal caudal row strongly keeled and ridge-like; mid-ventral scales strongly keeled, 29 to 30 (η) and 30 to 36 (δ) between axilla and groin.

The above characters consistently separate *sminthus* from *crassulus* in Honduras; all other characters of scalation show overlap or are too subjective to be of use. Despite the obvious differences between *crassulus* and *sminthus* in Honduras, specimens of the *crassulus* group from Guatemala and México

have a bewildering array of admixtures of the distinctive characters observed in Honduras, except that nowhere outside of Honduras and El Salvador (see below) are smooth or weakly-keeled mid-ventrals encountered. The inter-relationships of the populations that have received the names *smintus*, *crassulus*, *haguei*, and *anisolepis* are exceedingly complex, and after examining specimens of all 4 supposed forms from México to Honduras, we are unable to suggest a satisfactory arrangement. In our opinion extensive studies of live animals in the field will be necessary to clarify the status of these anoles.

We have examined 2 specimens (UMMZ 117647, MCZ 57280) from Miramundo, Santa Ana, El Salvador, identified by Robert Mertens (Rand, 1957) as *Anolis heteropholidotus*, which was described by Mertens (1952a) from this locality. Miramundo lies just across the valley of the Río Lempa from the *A. smintus* locality in the Departamento de Ocotepeque, Honduras, and the 2 specimens mentioned above from Miramundo are definitely referable to *smintus*. We suggest that *Anolis heteropholidotus* be tentatively considered a junior synonym of *Anolis smintus*, until such time as a complete study of the *crassulus* group is undertaken.

Two other species need to be mentioned in connection with *Anolis smintus*. *Anolis bouvierii*, described by Bocourt (1873) from Escuintla, Guatemala, was suggested by Stuart (1955) as a possible member of a group also containing *Anolis cobanensis* and *A. heteropholidotus*. Since we consider *heteropholidotus* to be a synonym of *smintus*, it was necessary to examine specimens of both *cobanensis* and *bouvierii*. *Anolis bouvierii* is known only from the holotype (MNHN 2464), and we were fortunate in being able to examine this specimen through the kindness of Jean Guibé, Museum Natural d'Histoire Naturelle, Paris, and Jay M. Savage, University of Southern California. The holotype is a male in excellent preservation, and differs in several features from the *crassulus* group. *Anolis bouvierii* has conical dorsal scales, not distinctly differentiated from the laterals (about 10 rows of keeled, distinctly enlarged dorsals in the *crassulus* group); no enlarged postanal scales in *bouvierii* (row of enlarged postanals in males of *crassulus* group); 68 ventrals between axilla and groin in *bouvierii* (no more than 50 ventrals between axilla and groin in males of *crassulus* group); a very large dewlap, extending posteriorly to about halfway between axilla and groin in *bouvierii* (dewlap moderate in size, not or barely extending posteriorly beyond axilla in males of the *crassulus* group); color of *bouvierii*, in preservative, light green with brown splotching (due to uneven color change) dorsally, the throat and sides of neck black, with some black

extending onto shoulders (color and pattern variable in *crassulus* group, but never approaching that of *bouvierii*). *Anolis bouvierii* is clearly not related to the *crassulus* group, nor in our opinion does it have any close relationship to *cobanensis* or any other anole from northern Middle America.

Stuart (1955) based the supposed relationship of *A. cobanensis* and *A. heteropholidotus* (= *smintus*) on the presence of smooth to weakly keeled ventrals in the two species. Examination of more specimens of *smintus* than were available to Stuart indicates that there is a tendency toward strong keeling in all but the mid-ventral scales, so that *smintus* approaches having the strongly keeled ventrals characteristic of all other species of the *crassulus* group. In addition to the difference in ventrals between *cobanensis* and the *crassulus* group, there are no enlarged postanal scales in *cobanensis* (present in all *crassulus* group males), the dorsals are not abruptly enlarged from the laterals in *cobanensis* (abruptly enlarged in *crassulus* group), the ventrals range from 53 to 61 between the axilla and groin in both sexes of *cobanensis* (no more than 50 ventrals between axilla and groin in either sex in *crassulus* group), and the loreals range from 8 to 10 in *cobanensis* (maximum of 6 in *crassulus* group).

Sphaerodactylus dunni Schmidt

This species was previously known only from the type, described by Schmidt (1963) from Río Naco, near Cofradía, Departamento de Cortés, Honduras. In July 1968, we collected 3 specimens (LACM 47302-04) of this species, 12 km S La Ceiba, Departamento de Atlántida, where they were found in the daytime among the leaves on the ground along a small stream. The junior author secured another specimen (LSUMZ 22450) in August 1969, along the Río Cristales at an elevation of 150 to 200 m in the mountains above Trujillo, Departamento de Colón. This individual was found in the morning moving among the leaves on the ground along a trail near the river.

Scale counts and measurements for the holotype (Schmidt, 1936) and for the additional specimens in our collections are in close agreement. As the type description was based on a preserved specimen, we offer the following color and pattern description, a composite of notes made on two males (LACM 47303, LSUMZ 22450) in life. Dorsum brown with light transverse markings, which decrease in intensity posteriorly. Nape region black, grading into orange-brown laterally and anteriorly, crossed by three white bands, which are more or less confluent with a lateral white stripe on each side. Dorsal surface of the head orange-brown to light brown, with

a reddish-brown nasal blotch and a dark reddish to orange-brown parietal blotch, outlined by a Y-shaped white to pinkish-white marking, the arms of which are confluent with the light ground color of the head; lateral head color orange-brown, with pinkish-white upper labials. Chin white with orange to brown reticulate or streak-like markings; throat with a mixture of white, orange, and brown scales. Venter light brown. Tail orange-brown to reddish-brown dorsally and orange ventrally. Iris red.

Bothrops bicolor Bocourt

This species of arboreal pit viper is a relatively rare snake, and in his description of *Bothrops rowleyi*, Bogert (1968) was able to gather data on only 7 specimens of *B. bicolor*. At 9:00 P.M. on 28 June 1968, we collected a juvenile male of *bicolor* (LSUMZ 23821), 23 km E Nueva Ocotepeque, Departamento de Ocotepeque, at an elevation of 1730 m. At the spot where this snake was collected, there is a small stream running through second growth cloud forest, and patches of apparently virgin cloud forest (Lower Montane Moist Forest formation of Holdridge, 1962) are present in the area. The snake was lying on a low branch overhanging the stream.

Our specimen agrees with the description of *bicolor* given by Bogert (1968). There are 164 ventrals, 61 subcaudals, 21-21-15 dorsal scale rows, 9-10 supralabials, and 10-10 infralabials.

In life the color pattern was: dorsum chartreuse green, dorsal blotches grayish-green, lateral blotches sky blue; venter very light green, finely peppered with darker flecks, lateral edges of most ventrals chartreuse green; head chartreuse green with two dark grayish-green bands extending posteriorly from the snout to the angle of the jaw, a similar but lighter band extending from the posterior edge of the eye to the angle of the jaw; some additional dark grayish-green mottling between the two bands on top of the head; eye chartreuse green with heavy black reticulations.

Although Bogert (1968) stated that *Bothrops bicolor* lacks any markings, color notes made in life on LSUMZ 11638 (the only other specimen known from Honduras) by the collector, Burt L. Monroe, state that the dorsum was grass-green with powder blue chevrons and the venter was yellowish-green.

Dryadophis dorsalis (Bocourt)

Lynch and Smith (1966) suggested that *Dryadophis dorsalis* be considered a subspecies of the wider-ranging *Dryadophis melanolomus*. This suggested change was made on the basis of the pattern of a

juvenile from the mountains above Zanatepec, Oaxaca, México, resembling the pattern depicted by Stuart (1941) for *dorsalis*, and on the fact that adults from the same area are stripeless and are allocated to *melanolomus*. The distribution of the two species as pictured by Stuart (1941) is suggestive of a subspecific relationship, but recent collecting in Honduras has demonstrated overlap in the ranges of *dorsalis* and *melanolomus* without intergradation. In 1968 we collected a juvenile and an adult *dorsalis* (LSUMZ 23822-23) at Finca Los Naranjos (= Finca Fé), 2 km W El Jaral, Departamento de Cortés, and the same year Ernest A. Liner collected a juvenile *melanolomus* (EAL 2200), 6 km N Agua Azul, Departamento de Cortés. Both localities are on or near the edge of Lago de Yojoa, and are about 4 km apart.

Dryadophis melanolomus in Honduras occurs at sea level to 750 m in lowland rainforest, subtropical rainforest, scrub and thorn forest, and lowland pine savanna, whereas *dorsalis* occurs from 750 to 1900 m in subtropical rainforest, upland pine and pine-oak forest, and cloud forest. The area where the ranges of the two overlap is dominated by forest that is ecotonal between the lower, warmer rainforest and the higher, cooler cloud forest (this intermediate type is designated the Subtropical Wet Forest formation by Holdridge, 1962).

Adult *dorsalis* are olive green dorsally and yellow grading to green ventrally. A black mid-dorsal stripe occupies the mid-dorsal scale row, and runs the length of the body. Juvenile *dorsalis* are olive green on the anterior quarter of the body, grading to rust brown on the middle half, and grading again to olive green on the posterior quarter of the body. The blotches on the anterior portion of the body are the most distinct, dark olive green in color outlined with black, and the dorsal blotches alternate with the lateral ones, contrary to Stuart's (1941) description. The dorsal blotches are connected medially to a wavy, black mid-dorsal line, which continues to the end of the tail.

Adult *melanolomus* are chocolate brown, light brown, or grayish-brown with vague indications of darker stripes on scale row 3, and occasionally on rows 6 to 9. Juvenile *melanolomus* have a similar ground color to that of the adults, with light bars about one-half scale in width extending completely across the dorsum. This is the type of pattern figured by Stuart (1941, pl. 1, fig. 6) for *D. dorsalis* and *D. melanolomus laevis*.

At least some juvenile *dorsalis* have a pattern of alternating dorsal and lateral blotches, and we have shown that *melanolomus* and *dorsalis* are sympatric and distinct in the Lago de Yojoa region of Honduras. Therefore, we prefer to regard *dorsalis* as a

species distinct from *melanolomus*, especially in view of the somewhat confused situation presently existing with material from the Tehuantepec region of México. Lynch and Smith (1966) have discussed this situation and regard the subspecific status of the circumisthmal populations of *melanolomus* as in doubt, and their allocation of the Zanatepec juvenile to *dorsalis* is in need of confirmation.

Lampropeltis triangulum Lacepede

A specimen (LSUMZ 23824) from 4.5 km SE Catacamas, Departamento de Olancho, is unusual in having a color pattern composed only of red and black rings. In life the dorsum was dark red with 41 black body bands and 10 black tail bands. The venter was reddish-orange.

We are aware of only one other such specimen having been reported; Dunn and Bailey (1939) recorded a bicolor *Lampropeltis triangulum micropholis* from near the Canal Zone in Panamá. Our specimen was taken at night in a partially flooded cornfield.

Ninia atrata (Hallowell)

Prior to our discovery of this species in Honduras, *Ninia atrata* was not known north of Costa Rica (Burger and Werler, 1954; Scott, 1969). During the summer of 1968, we collected 3 specimens (LSUMZ 23825-27) from under logs in a clearing in cloud forest (Lower Montane Moist Forest formation of Holdridge, 1962), 21 km E Nueva Ocotepeque, Departamento de Ocotepeque. In life the color pattern was: dorsum gray; venter cream with some gray flecking on the posterior portion, especially the underside of the tail; supralabials cream; iris black; no evidence of a nuchal band.

The absence of a light nuchal band in the Honduran specimens is a point of dissemblance with typical *atrata* (Burger and Werler, 1954; Lynn, 1959; Roze, 1966; Taylor, 1951). Roze (1966), however, noted that the nuchal band "at times, may be inconspicuous or absent" (translation ours) in Venezuelan individuals. We have compared the Honduran material with two specimens of *atrata* from the provinces of Bocas del Toro (KU 112621) and Darién (KU 112622) in Panamá, and can note no difference in color except for the presence of the typical nuchal band in the Panamanian specimens. The nuchal band of KU 112621 is orange and that of KU 112622 is cream. In addition, comparison of the hemipenes of KU 112622 with those of LSUMZ 23825 and LSUMZ 23827 reveals no difference in structure. Scale counts for the Panamanian and Honduran specimens fall within, or are

close to, the ranges given for *atrata* by Burger and Werler (1954). The Honduran specimens, all males, have 142 to 146 ventrals and 59 to 60 subcaudals.

In view of the fact that only the lack of a nuchal collar distinguishes the Honduran specimens from typical *atrata*, and since some Venezuelan specimens also lack collars, we regard the Honduran specimens as representatives of *Ninia atrata*. Whether the Honduran population is characteristically collarless cannot be answered until more material becomes available.

We accept the use of the name *atrata* instead of *lansbergi* for this species of *Ninia*, in accordance with the decision presented in Opinion 644 of the International Commission on Zoological Nomenclature (Bull. Zool. Nomencl., 20: 26) to suppress the combination *Coluber atratus* Gmelin, 1768 and to validate the combination *Coluber atratus* Hallowell, 1845.

Rhadinaea kinkelini Boettger

This snake has previously been recorded only from Nicaragua by Boettger (1898) in the type description. On 27 June 1968, we collected a single specimen (LSUMZ 23828) of *R. kinkelini* from under a log in a clearing in cloud forest (Lower Montane Moist Forest formation of Holdridge, 1962), at an elevation of 1900 m, 21 km E Nueva Ocotepeque, Departamento de Ocotepeque. This specimen was identified for us by Charles W. Myers, who is currently revising the genus *Rhadinaea*.

In life the color pattern was: dorsal ground color brown; dorsal scale rows 1 to 3 yellowish-cream with light brown flecking mostly along the edges of the scales, creating the impression of a stripe at the edge of each scale row; scale row 4 dark brown, row 5 tan, and row 9 brown with a very dark brown stripe down the center; head dark brown above with a tan collar about two scales long, two scales behind the parietals; supralabials mostly cream with dark brown edging; chin cream; anterior venter creamy yellow grading to cream posteriorly.

Our specimen is a male with 148 ventrals, 81 subcaudals, 17-17-17 dorsal scale rows, and 8 supra- and infralabials.

Sibon anthracops Cope

A male specimen (LSUMZ 23829) from 0.5 km N Coyoles, Departamento de Yoro, represents the first record for *Sibon anthracops* from Honduras and from the Caribbean versant; previously, the distribution was regarded as the Pacific slope of Costa Rica and Nicaragua (Peters, 1960). The range of *S. anthracops* is poorly known, and only 3 of the

specimens cited by Peters (1960) and one cited by Taylor (1954b) have precise locality data (all four are from Costa Rica).

Data for the Honduran specimen are: ventrals 166; subcaudals 82; dorsal scale rows 13-13-13; anal plate single; supralabials 7-8, with the 3rd, 4th, and 5th entering the orbit on the left side, and the 4th, 5th, and 6th entering on the right; no preoculars; loreal single, elongate, entering the orbit; postoculars 2-3; temporals 1 + 2/1 + 2; maxillary teeth 15; total length 664 mm, tail length 153 mm.

In life the color pattern was: dorsum white with 19 black body bands, some extending onto venter to form rings, and others not meeting on venter; 15 black bands on tail; scale rows 3 to 11 orange between the black body bands; orange dorsal coloration most pronounced and extensive posteriorly, and continuing onto tail; venter white; head mostly black, with this coloration extending laterally almost to lip, posterolaterally as far as the anterior half of the anterior temporal, and posteriorly to the anterior three-fourths of the parietals; first white interspace extending to second scale behind parietals; chin white except for black markings on mental, first three infralabials, and anterior portion of anterior chin shields.

Our specimen was collected at 8:35 P.M. on 28 July 1967, about 3 m in a tree (*Acacia*) in an area of second-growth thorn forest (Tropical Arid Forest formation of Holdridge, 1962).

Sibon carri (Shreve)

Sibon carri was previously known only from 4 specimens from El Zamorano, Departamento de Francisco Morazán, Honduras (Peters, 1960), and one specimen from San Salvador, El Salvador (Mertens, 1952b).

On the night of 18 June 1968, we collected 2 females of this species, one from 5 km WNW Choluteca, Departamento de Choluteca (LSUMZ 23830), and the other from 3 km E Goascorán, Departamento de Valle (LSUMZ 23831); both of these localities are in an area of mixed scrub forest (Tropical Dry Forest formation of Holdridge, 1962). Both specimens agree well with the description of the species given by Peters (1960). Data for our specimens are (LSUMZ 23830 given first, LSUMZ 23831 second): ventrals 169, 170; subcaudals 43, 46; dorsal scale rows 13-13-13 in both; anal plate single in both; supralabials 6-6, 3rd and 4th entering the orbit in both; infralabials 7-6, 7-7; no preoculars; loreal single, elongate, entering the orbit in both; postoculars 1-1 in both; primary temporal absent, 5th supralabial in contact with

parietal and one secondary temporal in both; total length 379 mm, 421 mm; tail length 61 mm, 68 mm.

In life the dorsum was rust red with a series of irregular dark brown blotches, approximately equal in length to the interspaces. The venter was cream with scattered brown blotching. The vermiculate markings on the internasals and anterior portion of the prefrontals were cream, and the remainder of the dorsal head markings were reddish-orange.

Both of our specimens were found on a paved highway at night during rainstorms. Each individual contained two well-formed, elongate eggs, which ranged from 34.7 mm to 36.2 mm in length and from 6.8 mm to 7.3 mm in width.

Thamnophis cyrtopsis (Kennicott)

This gartersnake has not previously been recorded south of Guatemala (Stuart, 1963). Field work carried on in Honduras by Texas A and M University in 1967 and by us in 1968 has demonstrated the presence of *Thamnophis cyrtopsis* in the southwestern part of the country. The specimens were collected 21 km E Nueva Ocotepeque, Departamento de Ocotepeque (LSUMZ 23832-33), at La Esperanza, Departamento de Intibucá (TCWC 23817-19, LSUMZ 23835), and 5 km NNE La Esperanza, Departamento de Intibucá (LSUMZ 23834). All localities are within cloud forest or a mixed pine-oak-sweetgum forest (Lower Montane Moist Forest formation of Holdridge, 1962), at elevations of 1700 to 1900 m. Individuals were found in and around streams and ponds in cleared areas, and one specimen from the Ocotepeque locality contained the remains of a frog, *Plectrohyla* sp.

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OBSERVATIONS ON THE DISTRIBUTION AND ECOLOGY OF THE LITTORAL ASCIDIANS OF THE MAINLAND COAST OF SOUTHERN CALIFORNIA

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ABSTRACT: A study of the littoral ascidians of the mainland of southern California was conducted during the summer of 1970. The collecting sites are recorded and natural history notes on the 41 species listed are presented. The number of species found in each of the four areas studied along the coast (Santa Barbara, Pt. Dume, Palos Verdes-Los Angeles Harbor, and San Diego) suggests that the contemporary distribution of tunicates may be controlled more by water quality than by the availability of a physically suitable habitat.

The distribution, natural history, and specific composition of the ascidian fauna of southern California was first reported by Ritter and Forsyth (1917) and later reviewed and expanded by Van Name (1945). Both accounts were based on observations and collections made in the littoral zone and by dredging in the sub-littoral zone. A preliminary survey of this group of stenohaline organisms in southern California during the summer of 1970 resulted in some additions to the notes on the natural history of these organisms and a contemporary definition of their distribution.

Millar (1960) and others have advanced reasons for the abandonment of the generic name *Amaroucium* Milne Edwards, 1842, as used by Ritter and Forsyth (1917) and Van Name (1945), in favor of the use of the generic name *Aplyidium* Savigny, 1816, and this synonymy is adopted in this report.

METHODS

All collections from the intertidal zone to a maximum depth of 50 m were made south-east of Pt. Conception (lat. 34°, 27'N, long. 120°, 28'W) from areas of protected water and on the open coast. Collections were made by trawling with an 8 m otter trawl, by diving with the aid of SCUBA or during low tides. Specimens were brought into the

laboratory and narcotized with menthol overnight. Seawater formalin (5%) was added gradually over a 2-3 hour period. Specimens were stored in 5% seawater formalin until examined. The identification is based on Ritter and Forsyth (1917), Van Name (1945), and Abbott (1957).

RESULTS

The coast was arbitrarily divided into four collecting areas (Fig. 1-5), ranging from Santa Barbara south-east to San Diego. The species collected, collecting sites, and major firm substrate within each area are as follows:

SANTA BARBARA AREA

Figure 2

1. Naples Reef, 13-15 m, shale reef and rubble; 21 July 1970.
2. Ellwood pier, 1-11 m, concrete, wooden, and steel pier pilings; 21 July 1970.
3. Coal Oil Pt., 3-7 m, shale reefs; 21 July 1970.
4. Stern's wharf, 1-7 m, wooden pier piling; 30 July 1970, 18 August 1970.
5. Santa Barbara Harbor, 0-3 m, floats and wooden piling; 18 August 1970.

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Order Enterogona	
<i>Aplidium californicum</i>	1,3
<i>A. solidum</i>	1,3
<i>A. arenatum</i>	1
<i>Euherdmania claviformis</i>	2,3,4
<i>Polyclinum planum</i>	3
<i>Synoicum par-fustis</i>	3
<i>Didemnum carnulentum</i>	1,2,3,4
<i>Trididemnum opacum</i>	1,3
Unidentified didemnid	1
<i>Diplosoma macdonaldi</i>	3
<i>Clavelina huntsmani</i>	4
<i>Cystodytes lobatus</i>	2
<i>Distaplia occidentalis</i>	1,4
<i>Eudistoma psammion</i>	1,3
<i>E. ritteri</i>	3
<i>E. diaphanes</i>	3
<i>Sigillinaria aequali-siphonis</i>	1
<i>S. pulchra</i>	1
<i>Ascidia ceratodes</i>	1,2,3,5
<i>Chelyosoma productum</i>	4
<i>Ciona intestinalis</i>	5
<i>Perophora annectens</i>	2,3

Order Pleurogona	
<i>Botryllus</i> sp.	3,5
<i>Botrylloides</i> sp.	4,5
<i>Styela montereyensis</i>	1,2,3,4,5
<i>S. truncata</i>	2,3,5

<i>S. sp. (barnharti)</i>	4
<i>S. gibbsii</i>	3,4,4
<i>S. plicata</i>	4
<i>Pyura haustor</i>	2,3,4,5
<i>Boltenia villosa</i>	2,3
<i>Molgula verrucifera</i>	2,4
Number of species found: 32	

- PT. DUME AREA
- Figure 3
1. Paradise Cove, bait receiver, 1-2 m, nylon mesh fish net; 16 June 1970.

2. Little Dume Pt., 3-5 m, shale reef; 16 June 1970.

3. Leo Carrillo, 5 m, granitic rocks; 19 June 1970.

4. Paradise Cove, No. 8 reef, 10 m, shale reef; 26 June 1970.

5. Malibu Pt., 3 m, basaltic rocks; 28 June 1970.

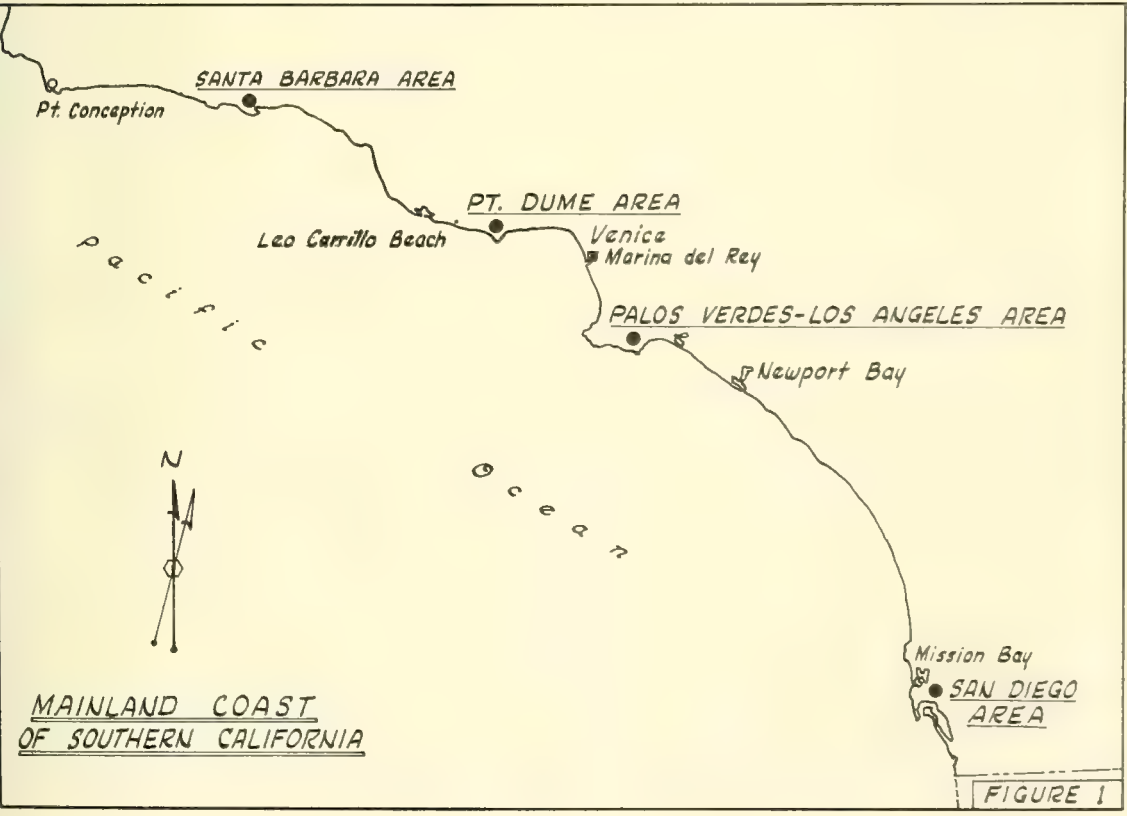
6. Pt. Dume rocks, 3-10 m, basaltic rocks; 2 July 1970.

7. Little Dume Cove, 3 m, shale reef; 2 July 1970.

8. Latigo Cove, 10 m, basaltic rocks; 26 August 1970.

9. West end of Zuma Beach, 6 m, granitic rocks; 1 September 1970.

Order Enterogona	
<i>Aplidium californicum</i>	2,3,4,5
<i>A. solidum</i>	3,7



<i>A. arenatum</i>	2,6
<i>A. propinquum</i>	2
<i>Euherdmania claviformis</i>	2,5
<i>Polyclinum</i> sp.	8
<i>Synoicum par-fustis</i>	9
<i>Didemnum carinulentum</i>	5
<i>Trididemnum opacum</i>	3,5,7
Unidentified didemnid	4
<i>Lissoclinum caulleryi</i>	6
<i>Clavelina huntsmani</i>	5
<i>Cystodytes lobatus</i>	7
<i>Distaplia occidentalis</i>	4
<i>Eudistoma psammion</i>	2,4,5,7
<i>E. ritteri</i>	2,3
<i>Pycnoclavella stanleyi</i>	5,7
<i>Sigillinaria aequali-siphonis</i>	2
<i>Ascidia ceratodes</i>	1,4,5
<i>Chelyosoma productum</i>	1,5,7
<i>Perophora annectens</i>	5
<i>Diplosoma macdonaldi</i>	8

Order Pleurogona

<i>Metandrocarpa taylora</i>	4
<i>M. dura</i>	2,7
<i>Styela montereyensis</i>	1,2,5
<i>S. truncata</i>	1,3,4,5,7
<i>Pyura haustor</i>	3

Number of species found: 27

REDONDO, PALOS VERDES,
LOS ANGELES HARBOR AREA

Figure 4

1. Palos Verdes, Long Pt. Marineland reef, 12 m, San Onofre Breccia; 18 June 1970.
2. Marineland pier, 3-5 m, wooden pilings; 15 June 1970.
3. King Harbor (Redondo Beach) boat slips, NE of harbor office, floats; 29 June 1970, 10 August 1970.
4. East end of King Harbor breakwater, 7 m, breccia rocks; 29 June 1970.
5. Rocky Pt., Palos Verdes, 7 m, San Onofre Breccia rocks; 29 June 1970.
6. Alamitos Bay, 1-3 m, floats and wooden pilings; 3 July 1970, 12 July 1970, 30 August 1970.
7. Los Angeles Harbor breakwater, 4-10 m, granitic and breccia rocks and debris; 3 July 1970, 12 July 1970, 30 August 1970.
8. Watchorn Basin, San Pedro, 0-2 m, floats and wooden piling; 15 August 1970.
9. Pt. Vicente, 7 m, breccia rocks; 15 August 1970.
10. Redondo, 45-50 m, sandy mud; 11 September 1970.
11. Abalone Cove, 6 m, breccia rock; 21 September 1970, 26 September 1970.
12. Resort Point, 5-10 m, breccia rock; 28 September 1970.
13. Abalone Cove, 3 m, breccia rock; 28 September 1970.

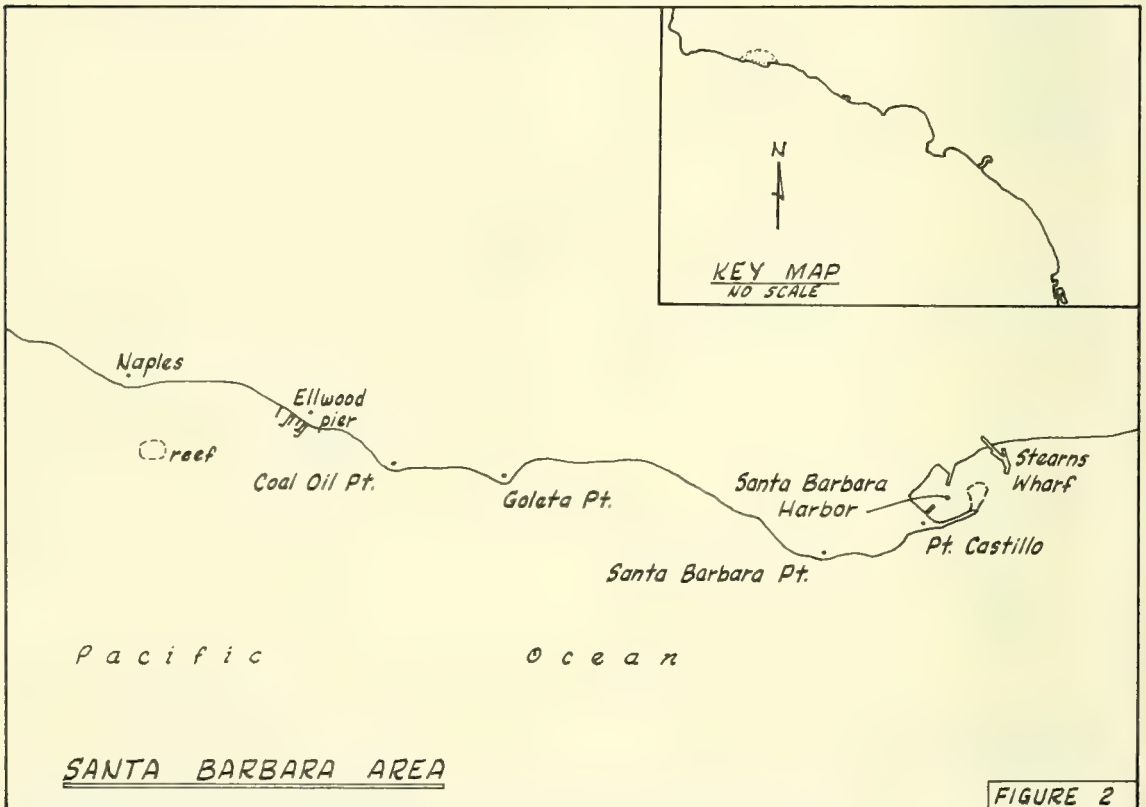


FIGURE 2

Order Enterogona

<i>Aplidium californicum</i>	1,4,6,7
<i>A. solidum</i>	2
<i>A. propinquum</i>	2,13
<i>Euherdmania claviformis</i>	13
<i>Synoicum par-fustus</i>	12
<i>Didemnum carinulentum</i>	3
<i>Clavelina huntsmani</i>	9,12
<i>Distaplia occidentalis</i>	8
<i>Cystodytes lobatus</i>	2,5,7,11,12
<i>Eudistoma psammion</i>	13
<i>Ascidia ceratodes</i>	3,7,11,12
<i>Ciona intestinalis</i>	3,6,10
<i>Diplosoma macdonaldi</i>	3

Order Pleurogona

<i>Metandrocarpa taylori</i>	11
<i>Botrylloides</i> sp.	3,6,7
<i>Botryllus</i> sp.	3,6
Unidentified styelid	6
<i>Styela truncata</i>	2,7,11,12
<i>S. sp. (barnharti)</i>	3,6
<i>S. gibbsii</i>	7,8,11
<i>S. plicata</i>	3,6,8
<i>Halocynthia igaboja</i>	11
<i>Pyura haustor</i>	1,5,7,12
<i>Eugyra arenosa</i>	10

Number of species found: 24

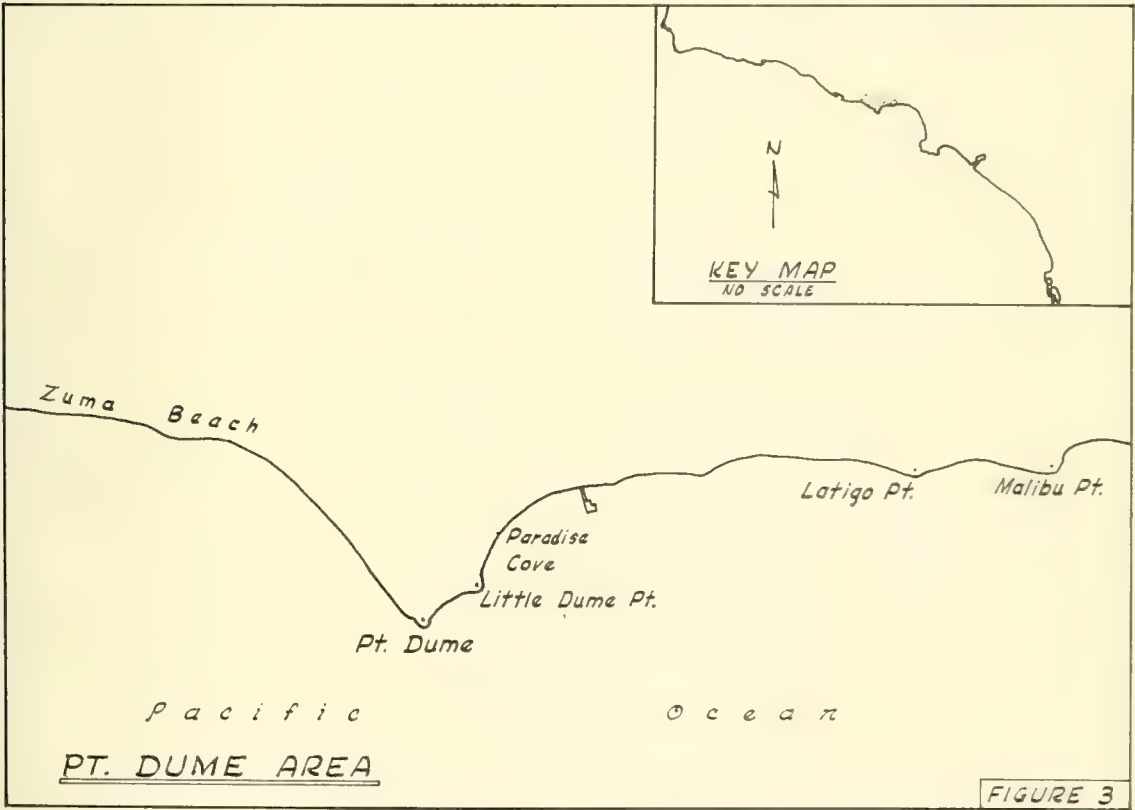
SAN DIEGO AREA

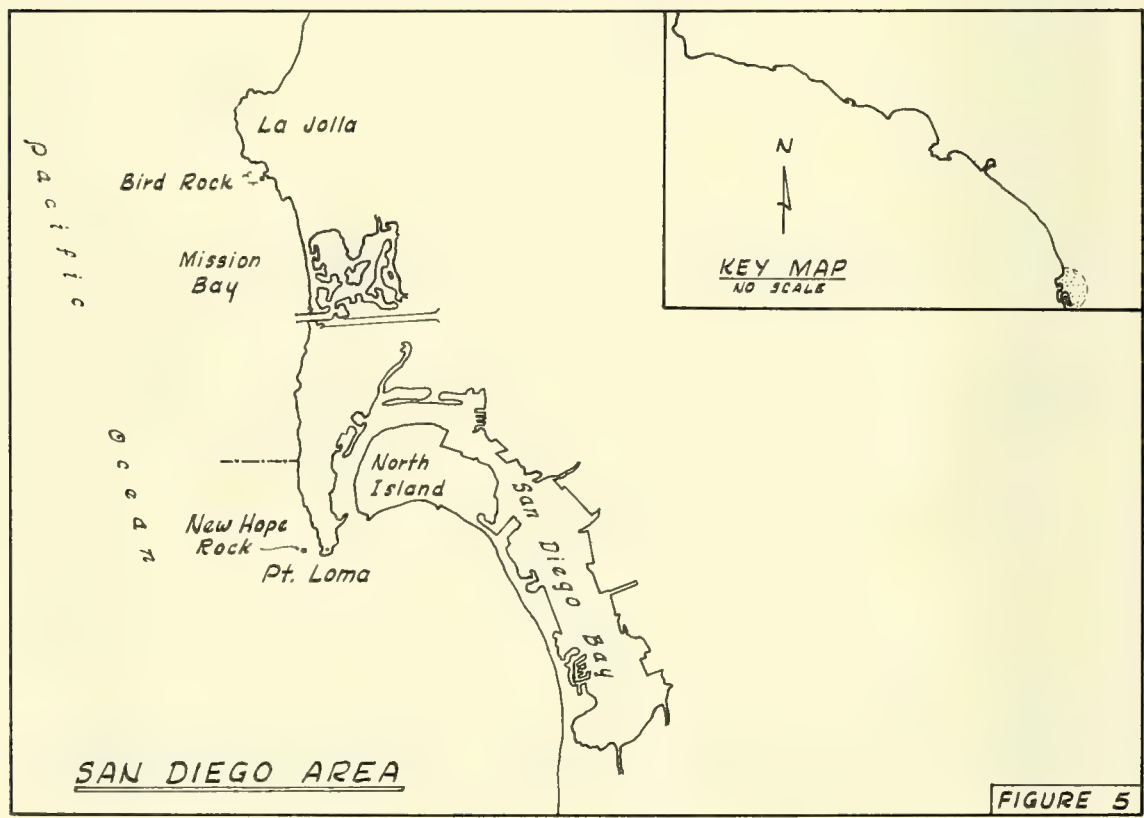
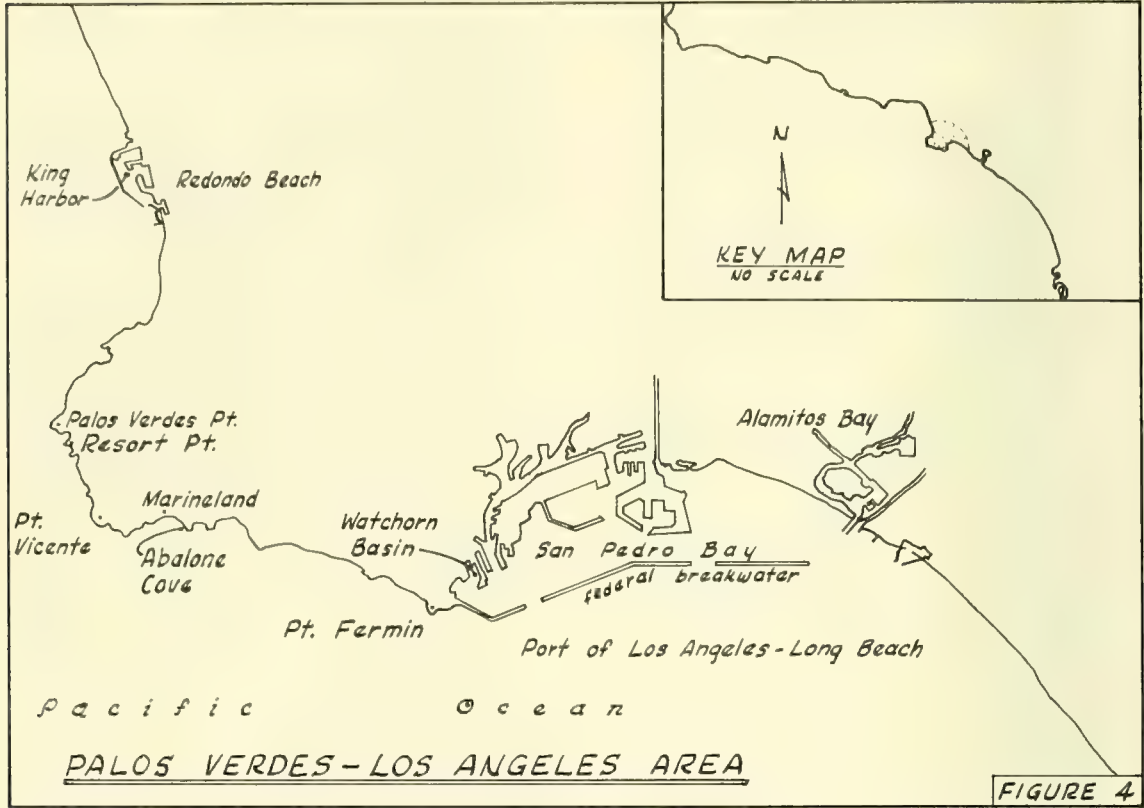
Figure 5

1. Dana marina, Mission Bay, 0-1 m, floats and wooden pilings; 5 June 1970.
2. Pt. Loma, 27 m, shale rock, transect opposite intake line for naval station (Fig. 5); 11 June 1970
3. 23 m, shale rock; 11 June 1970
4. 20 m, shale rock; 11 June 1970.
5. 14 m, shale rock; 11 June 1970.
6. 7 m, shale rock; 11 June 1970.
7. Entrance channel east jetty inside Mission Bay, 2-3 m, breccia rock; 11 June 1970.
8. Ventura Bridge, 3 m, wooden pilings; 14 June 1970.
9. Ventura Bridge, 0-5 m, rock rip rap; 18 June 1970, 12 September 1970.
10. New Hope Rock Transect line Pt. Loma, 25-30 m, shale rock; 21 October 1970.
11. 15 m, shale rock; 21 October 1970.
12. 10 m, shale rock; 21 October 1970.
13. 3 m, shale rock; 21 October 1970.
14. Bird Rock, La Jolla, intertidal, cobble bed; 28 November 1970.

Order Enterogona

<i>Aplidium californicum</i>	1,3,7
<i>A. solidum</i>	2
<i>Euherdmania claviformis</i>	-
<i>Polyclinum planum</i>	2





<i>Synoicum par-fustis</i>	2,10
<i>Didemnum carnulentum</i>	1,4,7
<i>Clavelina huntsmani</i>	11
<i>Trididemnum opacum</i>	2
<i>Diplosoma macdonaldi</i>	1
<i>Lissoclinum caulleryi</i>	7
<i>Distaplia occidentalis</i>	1
<i>Eudistoma psammion</i>	3,4,7
<i>E. diaphanes</i>	4
<i>E. ritteri</i>	4,5
<i>Cystodytes lobatus</i>	11
<i>Ascidia ceratodes</i>	2,4,7,9
<i>Chelyosoma productum</i>	3,10,11
<i>Ciona intestinalis</i>	1
<i>Perophora annectens</i>	3

Order Pleurogona

<i>Metandrocarpa taylora</i>	13,14
<i>Botryllus</i> sp.	1,6
<i>Botrylloides</i> sp.	1,7
<i>Styela montereyensis</i>	1,5,7,10,11
<i>S. truncata</i>	8
<i>S. sp. (barnharti)</i>	1
<i>S. gibbsii</i>	7,9,10
<i>S. plicata</i>	1
<i>Pyura haustor</i>	2,7,8,9
<i>Boltenia villosa</i>	9,10,11
<i>Molgula verrucifera</i>	7

Number of species found: 30

ANNOTATED SPECIES LIST

Aplidium californicum (Ritter and Forsyth). Specimens were collected from each of the four areas, often in abundance. Colonies were taken in the bathymetric range of 2-27 m and were found growing over rocks, worm tubes, algae, and other substrates. Zooids reached a size of 5-8 mm in length and were often organized into definite systems. The colonies ranged in color from opalescent white to yellow-orange. The breeding season is at least throughout the summer months as larvae and/or embryos (4-6) were found in some individuals in each collection.

Aplidium solidum (Ritter and Forsyth). Specimens were collected from the coastal areas surveyed and were found growing over worm tubes, kelp holdfasts, and rocks. The zooids measured to 10 mm in length; they ranged in color from orange to nearly white. Some animals in each colony had larvae and/or embryos in their atrial cavities; the embryos in the colony collected 15 June appeared to be more advanced than any of the other specimens of this species collected during the summer of 1970.

Aplidium propinquum (Van Name). Colonies, made up of several sand covered lobes, were taken

at Little Dume Pt., at 5 m growing over worn tubes and at Palos Verdes, Marineland Pier, 5 m, on rock and pier piling. The zooids measured 17-27 mm in length (the post abdomen ranged from 10-20 mm) and were an orange-red color. This represents an extension of the range of this species to southern California (Abbott, 1957).

Aplidium arenatum (Van Name). Colonies were collected from Santa Barbara and Pt. Dume down to a depth of 5 m; they were found growing over sponge, algae, and other surfaces. Zooids reached an overall length of 14 mm (the thorax and abdomen measured about 5 mm) and were white. Animals collected in June and July were found with larvae in their atrial cavities.

Euherdmania claviformis Ritter. Specimens were collected at each of the areas surveyed, from the intertidal down to a depth of 12 m; only one colony was found in the Palos Verdes region. These social ascidians, with zooids measuring 15-20 mm, were taken growing with hydroids and bryozoans. The animals from Ellwood pier were covered only very lightly with sand. Trason (1957) gives the breeding season as July to September, with the peak in August. Animals collected on 16 June had a characteristic arrangement of embryos in a longitudinal series in the oviduct.

Polyclinum planum (Ritter and Forsyth). Colonies were taken from Pt. Loma, Latigo Cove, and Coal Oil Pt. The bathymetric distribution ranged from 5-30 m. The colonies are reddish in color and lightly covered with sand; they often become quite large, measuring up to 20 cm in width. The zooids have a length of 7 mm. The colonies narcotized well with menthol.

Polyclinum sp. An unidentified species of this genus was collected at a depth range of 5-10 m at Latigo Cove in the summer of 1970 and 1971. The colony is of 4-15 cm in height and of a more globular form than *P. planum*. It is grayish white in color.

Synoicum par-fustis (Ritter and Forsyth). Specimens were collected at Pt. Loma (27 m), Coal Oil Pt. (5 m), and at Zuma Beach (6 m). Zooids averaged 10 mm in length; the colonies were 60-115 mm in height. A colony collected at Zuma Beach was nearly twice as long as reported for the maximum size of colonies of this species (Van Name, 1945). Colonies taken from Coal Oil Pt. and Zuma Beach were orange-red; some from Pt. Loma were white. This species narcotized well with menthol. The breeding season is at least June and July as embryos were found in the atrial cavities of individuals at this time of year. Generally, zooids had 1 or 2 well-developed tadpoles and several embryos in the atrial cavity.

Didemnum carnulentum Ritter and Forsyth. Specimens were collected in each of the areas surveyed, down to a depth of 20 m. Colonies, encrusting and less than 4 mm thick, were found growing on various algae, with a colony of *Euherdmania*, and on rocks. The yellow-orange zooids were less than 2 mm in length. Colonies were also taken in abundance growing on the carapace of decorator crabs, *Loxorhynchus crispatus*, at Santa Barbara. No indication of breeding activity was seen although Ritter and Forsyth (1917) mentioned that the zooids contained tadpoles in June.

Trididemnum opacum (Ritter). Specimens were taken from all areas but the Palos Verdes-L.A. Harbor area. The bathymetric range is from surface to 27 m. Colonies of this gray ascidian were found growing on kelp holdfasts, hydroids, and worm tubes; they ranged in thickness from 1-4 mm.

Diplosoma macdonaldi Herdman. This species was found from Santa Barbara to San Diego, at all areas surveyed, on floats, pier pilings, mussel shells, and kelp down to 10 m. The zooids are brown and measure about 1 mm in length. A colony taken from King Harbor (10 August) had numerous zooids in various stages of budding. Animals collected on 21 July had larvae free in the common test. This species is characterized by a very fragile, gelatinous test.

Lissoclinum caulleryi (Ritter and Forsyth). Colonies were taken from San Diego and Pt. Dume growing on kelp, hydroids, and rocks. The zooids measured to 1.5 mm in length. A colony from San Diego on 11 June had many larvae and large eggs free in the test; those specimens collected in July appeared to be sexually mature.

Clavelina huntsmani Van Name. This species was taken in each of the areas surveyed. It is characterized by a clear test and a bright pink pharynx. It grows on rocks in areas of vigorous water movement. A colony from Santa Barbara was surrounded by a sponge. The zooids grow to over 30 mm in length. Van Name (1945) found this species to occur on an annual basis and to be in reproductive condition at Pacific Grove from June to September.

Cystodytes lobatus (Ritter). This species was collected in each of the areas surveyed. Colonies of up to 25 cm in width were found growing on worm tubes, kelp holdfasts, shells, and rocks; individual zooids were 2.5 mm in length. Individual colonies ranged in color from off-white through orange-tan to pink. Animals collected in June and July had larvae and eggs in their atrial cavities. This is the dominant species found in the collections from the Los Angeles-Long Beach Federal breakwater.

Distaplia occidentalis Bancroft. Colonies were found in all of the areas surveyed down to 15 m on

mussel shells, rocks, piling, and other surfaces. Zooids were about 2 mm in length. Colonies were found with larvae in them throughout the summer. Ritter and Forsyth (1917) pointed out that the color of the colony becomes darker with age. The colors of observed colonies of this species ranged from cream-white to dark red-brown.

Eudistoma diaphanes Ritter and Forsyth. Colonies of this opalescent white ascidian were taken from San Diego and Coal Oil Pt. down to a depth of 20 m. They were found growing on algae and over clam shells. Colonies reached a width of 25 mm, zooids a length of 3 mm. Colonies collected on 21 July had larvae and eggs present in them.

Eudistoma psammion Ritter and Forsyth. This species was collected in all of the areas surveyed. The bathymetric range extended from the intertidal to a depth of 27 m. The sand-encrusted colonies are of a deep burgundy color and were found growing on rocks, *Chaetopterus* tubes, and kelp holdfasts. Colonies of *Euherdmania* were found growing with colonies of *Eudistoma psammion* taken from Malibu Pt. while these two joined with *Aplidium propinquum* at Abalone Cove. Zooids measured to 5 mm in length. Van Name (1945) gives the breeding season as June-July when the atrial cavities are often distended by large eggs and larvae. The colonies from Coal Oil Pt. had very little sand on their surfaces.

Eudistoma ritteri Van Name. Colonies were collected from Santa Barbara and San Diego between the depths of 3-20 m. Colonies were found with some sand over their surfaces, contrary to Van Name's description, and are dull gray in coloration. Zooids measured up to 3 mm in length. Van Name (1945) gave the breeding season as beginning in February-April, peaking in July, and declining in August.

Pycnoclavella stanleyi Berrill and Abbott. Specimens were found commonly at Little Dume Pt. on rocks and on *Cystoseira*, and in abundance at Malibu Pt. where they formed golden-orange mats up to 50 cm in width. This species was taken in depths ranging from 2-7 m.

Sigillinaria aequali-siphonis (Ritter and Forsyth). Colonies were found at Pt. Dume and Santa Barbara in 3-15 m of water. Light colored colonies were growing on algae and worm tubes. Zooids measured up to 6 mm in length. Eggs and larvae were present in the atrial cavities of animals in June and July. This species was reported from Pt. Loma by Turner, Ebert, and Given (1968).

Sigillinaria pulchra (Ritter). Two light colored colonies were taken in 15 m of water at Naples Reef, west of Santa Barbara; they were found growing on worm tubes. The zooids measured up to 15 mm

in length and there were four larvae in the atrial cavities of some individuals. This collection site serves as a range extension for the species as it is farther south than reported by Van Name (1945).

Ascidia ceratodes (Huntsman). Specimens were taken from every area studied in 0-27 m of water. The translucent light green or yellow animals measured 20-30 mm in length and were found growing on their sides on kelp holdfasts, pebbles, boat floats, pilings, and rocks. The external appearance is highly variable as it is controlled by the confinement of the surroundings. Only those specimens growing in the absence of confinement exhibit the form figured in Van Name (1945). Several of the specimens had a copepod crustacean living in their branchial basket; many of the copepods were carrying eggs. The gonad tissue of *A. ceratodes* appeared to be mature during the summer of 1970.

Chelysoma productum Stimpson. Specimens were taken from Santa Barbara to San Diego but they were not found in the Palos Verdes-L.A. Harbor area. The animals were collected in 2-27 m of water. The translucent individuals measured up to 15 mm across; specimens from Santa Barbara were noticeably larger than those from further south. The animals were found attached to abalone shells, kelp holdfasts, rocks, fish net, and corrugated aluminum sheeting.

Ciona intestinalis (Linnaeus). This species was only taken at Santa Barbara, in the L.A. Harbor area (Alamitos Bay), and in Mission Bay; however, it may be expected to be present during the summer and fall in all of the harbors along the coast. This light green, translucent species is generally found growing on concrete pilings, wooden pilings, algae, floats, rocks, mussels, and other solitary ascidians. Many animals will fall from floats or pilings and live out their lives lying on the bottom. Others will attach to various objects and grow along the open coast at depths below the zone of active wave surge down to a depth of at least 50 m. Specimens collected from under floats in Newport Bay measured up to 25 cm in length.

Perophora annectens (Ritter). This green or yellow-green species was collected in abundance from the Santa Barbara area; colonies were found growing on concrete and wooden pilings, algae, and rocks. A colony was also taken at Malibu Pt. Two specimens were taken in 27 m of water at Pt. Loma. The zooids measured up to 1.5 mm in length.

Unidentified styelid species. The individuals of this ascidian are joined together by stolons forming mats up to 4-6 cm in width which resemble colonies of *Perophora*. The animals measure 4-5 mm in length and are yellow in color. The colonies may have a light sand covering if taken near the surf

zone. A raphe is present along the intestine and the stomach has 11-12 ridges. The ovaries are in a row of 5 units along the right side of the body. There were numerous eggs and larvae in the peribranchial area. Specimens were collected at a depth of 4 m from the exposed side of the Venice breakwater on 22 August 1970, and from pier pilings in the protected waters of Alamitos Bay at depths to 4 m on 30 August 1970. This styelid closely resembles the description of *Alloecocarpa bacca*, which has been reported from the coast of Chile (Van Name, 1945).

Botryllus spp. These animals were collected in protected waters at Santa Barbara, Alamitos Bay, and Mission Bay from the surface to a depth of 3 m. This genus is also common in the Marina Del Rey in Venice, California. Specimens were found on any available firm substrate and narcotized well with menthol. *Botryllus tuberosus* and possibly other species were present. The colonies ranged in color from black to orange.

Botrylloides spp. Representatives of the genus were collected where protected water was found in each of the areas surveyed; they were found growing on mussels, hydroids, and other firm substrates from the surface to a depth of 4 m. *Botrylloides diegensis* and possibly other species were present.

Matandrocampa dura (Ritter). Specimens were collected only from the Pt. Dume area and were found growing over bryozoans, *Cystoseira*, and *Styela montereyensis*, down to 7 m. The zooids reached 4 mm in length; the colonies were a vivid red-brown color.

Metandrocampa taylori Huntsman. This orange-red species was collected at Paradise Cove (Pt. Dume area), Palos Verdes from 0-11 m, Pt. Loma in 3 m of water, and from the intertidal at Bird Rock, La Jolla. This tunicate was found growing on wood, shells, rock, and *Chaetopterus* tubes. Zooids were 3 mm in length. Two tadpoles and some advanced eggs were present in June. Abbott (1953) gave the breeding season as peaking in July and August. This record represents a southern range extension for this species on the mainland. It has also been reported from Catalina Island (Given and Lees, 1967).

Styela montereyensis (Dall). Specimens of this pinkish-red ascidian were not taken in the Palos Verdes-L.A. Harbor area but were found routinely elsewhere from the intertidal down to 17 m. The individuals were up to 25 cm in length and were growing on kelp. *Pyura haustor*, pilings, rocks, floats, shells, or any available hard substrate. *Styela montereyensis* is found with *S. sp. (barnharti)* in Santa Barbara Harbor and is the main channel at Mission Bay; thus *S. montereyensis* may grow in protected water. Many animals appeared sexually

mature during the summer months. A specimen was taken at Pt. Loma with a gravid pea crab in the branchial basket.

Styela plicata (Lesueur). This species was collected in protected waters from Santa Barbara to San Diego but isolated individuals may also be found in unprotected locations. The animals were found growing on pilings, boat floats, rocks, and hard objects on the bottom to a maximum depth of 8 m. They often reached a length of 10 cm. The species is opalescent white with brown striped siphons. It narcotized well with menthol. *Styela plicata* was one of three species of tunicates collected at Watchorn Basin in L.A. Harbor. It is recognized as having been introduced to southern California about 1945 (Abbott, pers. comm.), and is now locally abundant in protected waters throughout southern California.

Styela sp. (*barnharti*). Thanks to the insistence of J. Richard Whittaker (pers. comm.) that a problem exists in the accepted designation of this animal as *S.* sp. (*barnharti*), a close examination of the literature revealed that this species was not accurately described by Ritter and Forsyth (1917) nor Van Name (1945) (Abbott, pers. comm.). A description of this distinct species is now in preparation.

Individuals of this species were collected on floats, pilings, and rocks in Mission Bay and Santa Barbara Harbor from the surface to a depth of 7 m. This species is predominantly brownish in color. It may be found in protected waters anywhere in southern California where suitable water quality exists. Individuals grow to a length of about 20 cm. Sexually mature animals were seen at most times throughout the summer but spawning could not be induced in the laboratory.

Styela truncata Ritter. This species was taken from protected and exposed locations in all areas surveyed from the surface down to a depth of 12 m. Individuals were found growing on floats, worm tubes, shells, and sponges, as well as on other tunicates. The specimens were about 20 mm in length.

Styela gibbsii (Stimpson). Specimens were taken from semi-protected to protected sites at all four areas surveyed, from the surface to a depth of 30 m. They may be found attached to any firm substrate. Individuals reached 40 mm in length, and ranged in color from old rose with brown siphons to orange-red with red siphons. An animal from Pt. Loma carried the same type of copepod in its branchial basket as those found in *Ascidia ceratodes*.

Pyura haustor (Stimpson). This species was collected in all areas surveyed from the intertidal (Mission Bay) to 27 m (Pt. Loma). Animals ranged up to 12 cm in length and were generally lodged in

crevices, under rock ledges, in rip rap, or on pier pilings. This animal is always covered with a complex biota of fouling organisms and the only indication of the presence of this tunicate is its bright pink-red siphons. The animals from San Diego carried an amphipod in their branchial basket. This species probably breeds in the summer as indicated by the appearance of the gonads.

Halocynthia igaboja Oka. One specimen was collected at a depth of 6 m from under a rock at Abalone Cove, Palos Verdes. Van Name (1945) comments that this ascidian is fairly common about Catalina Island at a depth of 20-80 m. This finding is the first reported from the mainland of southern California, and it represents a new shallow depth record for the species.

Boltenia villosa (Stimpson). Specimens were taken in the Santa Barbara region, at Ellwood pier, and Coal Oil Pt. in 2-12 m of water, in Mission Bay at a depth of 4 m, and at Pt. Loma in 25 m of water. Individuals ranged up to 9 cm in length; Van Name (1945) described the size range as 3-6 cm. The tunic has a yellow-orange stalk and is bright brick red over the main body.

Molgula verrucifera Ritter and Forsyth. Individuals were collected from Santa Barbara, Venice, and San Diego. All specimens carried larvae in the peribranchial area. Specimens reached a maximum length of 7 mm. The cream color of the test is obscured by a gray-green layer of encrusting sand which makes the animals notably inconspicuous. Four of the specimens collected at Santa Barbara were taken from the carapace of a decorator crab, *Loxorhynchus crispatus*.

Eugyra arenosa (Alder and Hancock). Specimens were taken in abundance with the aid of an 8 m wide otter trawl off Redondo Beach in the depth range of 44-50 m. Most individuals were 10 mm in length; the largest were up to 20 mm. This record extends the bathymetric range and maximum size recorded for this species on this coast. The gonad was ripe; eggs and sperm were present in the gonaducts in early September. The atrial cavity of one specimen harbored a white flatworm 6 mm in length.

DISCUSSION

The four delimited areas surveyed along the mainland coast of southern California yielded a total of 40 recognized species of ascidians. This compares favorably with the 29 species noted as occurring in the littoral zone in this region by Ritter and Forsyth (1917). This listing does not include *Pyura mirabilis* Von Drasche, which has been collected by the senior author from the mainland of southern California, nor does it include one unidentified didem-

nid. Inclusion of these two species would bring the total to 43 species of ascidians from the littoral zone of the mainland of southern California. Undoubtedly further survey work in the field and additional descriptive work in the laboratory will add more ascidians to the list.

It is interesting to note that of the 39 species of ascidians listed by Abbott (1957) as occurring in the intertidal zone or located so that they are available near the surface (on floats) in central California, 16 species were found in the same situation in southern California. These include: an undescribed styelid, *Aplidium californicum*, *Ascidia ceratodes*, *Botryllus* sp., *Botrylloides* sp., *Metandrocarpa taylori*, *Ciona intestinalis*, *Distaplia occidentalis*, *Didemnum carinulentum*, *Euherdmania claviformis*, *Eudistoma psammion*, *Pyura haustor*, *Styela* sp., *S. montereyensis*, *S. plicata*, and *S. truncata*. Further, of the 39 species listed by Abbott (1957) or described by Abbott and Trason (1968) only 5 species have not been noted in southern California (*Cystodytes* sp., *Distaplia smithi*, *Eudistoma molle*, *Ritterella rubra*, and *Cnemidocarpa finmarkiensis*); thus, the majority of the littoral ascidians reported from the intertidal zone of central California are found southeast of Point Conception in the subtidal zone. The primary controlling factor limiting the appearance of these animals in the intertidal zone is probably temperature, since both water and air temperatures southeast of Point Conception along the shoreline average higher than those northwest of this break point in the distribution of intertidal marine organisms.

The present recorded difference between central and southern California with respect to the ascidian fauna amounts to about 10 species and one may question the quantitative significance of the statement of Van Name (1945) that Point Conception marks a "break point" in the distribution of these organisms. At this time and subject to further study, it would appear that a continuum of change in distribution of ascidians exists along the coastline of southern California which continues into central California.

Note has been made of the restriction of some species of tunicates to protected waters while others may be limited to the waters of the open coast. A comparison of the number of species found in either of these type habitats along the coast was made. A total of 10 species of tunicates was found in Santa Barbara Harbor and 16 species were found in Mission Bay, whereas 8 species were found in King Harbor, 8 species in Los Angeles Harbor, and 6 species in Alamitos Bay. In the adjoining areas of open coast, 27 species of tunicates were found in Santa Barbara, 26 species at Pt. Dume-Malibu,

and 23 species in San Diego, whereas only 10 species were found at Palos Verdes. Since the conservative oceanographic parameters of temperature and salinity, and the ranges for these parameters are essentially the same for all four collecting areas surveyed (Barkely, 1968), and since the physical habitats are similar in all four areas, these factors cannot account for the difference in numbers of species found in either the protected areas or on the open coast.

Water quality conditions along the coast line of the greater Los Angeles area have altered radically over the past 25 years. The reduction in abundance of certain species of benthic marine algae has been observed and the extirpation of *Macrocystis pyrifera* from the Palos Verdes Peninsula has been most significant (Young, 1964; Strachan and Koski, 1969; Gregg and Kiwala, 1970). The decline of *Macrocystis* and of other algae along the Palos Verdes Peninsula occurred during a period when the waste input into the waters bordering the peninsula increased rapidly; it is now on the order of 1.5 billion liters per day. About 2 billion liters of heated sea water discharged into the King Harbor Marina per day from the Redondo Beach power plant of the Southern California Edison Company. Los Angeles Harbor receives 29.5 million liters of sewage per day (Crippen and Reish, 1969) in addition to industrial wastes (largely brines) and some thermal wastes (Reish, 1959).

Since qualitatively and quantitatively equivalent waste loadings are not introduced into the water masses about the region of Santa Barbara and San Diego, it may be that the comparatively reduced number of species of tunicates found in the Palos Verdes area and in the bays in the area of greater Los Angeles demonstrates the presence of biologically unfavorable water quality in this area. It appears that the changes in water quality along the southern shoreline of Los Angeles County which have occurred and which currently exist are detrimental and limiting to sensitive species of both algae and benthic invertebrates.

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BENTHONIC FORAMINIFERA OF THE ARDATH SHALE AND
STADIUM CONGLOMERATE (EOCENE), SAN DIEGO BASIN, CALIFORNIA

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ABSTRACT: Suites of samples collected from the Ardath Shale and Stadium Conglomerate, San Diego, California were analysed for benthonic foraminifera. The Ardath Shale contains a classic "Ulatisian" benthonic foraminiferal assemblage characterized by large percentages of *Cyclammina*, *Reophax*, *Gyroidina*, *Bulimina*, and *Eponides*. The benthonic assemblage suggests deposition of the Ardath Shale in upper middle bathyal water depths (600-1500 m). Planktonic foraminifera indicates an early Middle Eocene age.

A "Narizian" benthonic foraminiferal assemblage is characteristic of the Stadium Conglomerate. Arenaceous genera are few in number (mainly *Gaudryina*). Species of *Anomalina*, *Hanzawaia*, *Nonion*, *Melonis*, and *Cibicides* dominate the benthonic fauna. Such a faunal composition is suggestive of inner shelf deposition (0-60 m). A late Middle Eocene age is indicated by planktonic foraminifera.

The pre-Tertiary geology of the San Diego Basin (Fig. 1) was discussed by Hertlein and Grant (1944, 1954), Milow and Ennis (1961), Peterson and Nordstrom (1970), and Moore and Kennedy (1970). Hanna (1926) proposed the term "La Jolla Formation" for the entire Paleogene sedimentary sequence of the San Diego Area. Milow and Ennis (1961) divided the "La Jolla Formation" into the Delmar, Torrey, Rose Canyon, unnamed unit, and Poway Formations. Peterson and Nordstrom (1970), however, retained the usage of "La Jolla Formation" for the lower Tertiary strata. Kennedy and Moore (1971) divided the La Jolla group into the Mount Soledad Formation, Delmar Formation, Ardath Shale, Scripps Formation, Friars Formation and also divided the Poway Formation into the Stadium Conglomerate and Mission Valley Formation.

This study is concerned with the benthonic foraminifera of the Rose Canyon Formation and the superjacent Poway Formation. The planktonic foraminifera, age relationships, and general correlation of the Rose Canyon and Poway Formations are discussed more fully elsewhere by Steineck and Gibson (1971, 1972), Steineck, Jervey, and Gibson (1971) and Steineck (1971).

Hanna (1926) and Cushman and Hanna (1927) established an Eocene age for the Rose Canyon member of the "La Jolla Formation" and the Poway Conglomerate. A late "Tejon" age was assigned to the Poway Formation by Stock (1937) on the basis of vertebrate remains. Foraminiferal faunas studied by Cushman and Dusenbury (1934) were interpreted also as being late Eocene in age. Clarke and Vokes (1936), evaluating molluscan faunas, and Laiming (1943), evaluating foraminiferal assem-

blages, ascertained a "Domengine" age (upper Middle Eocene) for the Rose Canyon Formation. Laiming (1943) retained a "Tejon" age for the Poway Formation. Mallory (1959) presented data which assigns the Rose Canyon Formation to the "Ulatisian" stage (Middle Eocene) and the Poway Conglomerate to the "Narizian" stage (late Eocene). Milow and Ennis (1961) suggested a synchronization of both the Rose Canyon and Poway Formations with the middle Eocene of the Gulf Coastal Plain; however, the authors do not make explicit the reasons for such an age assignment. Bukry and Kennedy (1969) assigned an early Middle Eocene age to the Rose Canyon Formation on the basis of nannoplankton floras. Kennedy and Moore (1971) divided the La Jolla group and Poway Formation into various formations and assigned the Mount Soledad Formation, Delmar Formation, Ardath Shale, and portions of the Scripps and Friars Formations to the Middle Eocene and the remaining portions of the Scripps and Friars Formations as well as the Stadium Conglomerate and Mission Valley Formation to the Upper Eocene.

METHODS

Natland (1933) established benthonic foraminiferal assemblages which are characteristic of distinct water depth ranges. Phleger and Parker (1951), Bandy (1963a), and Bandy and Arnal (1957) con-

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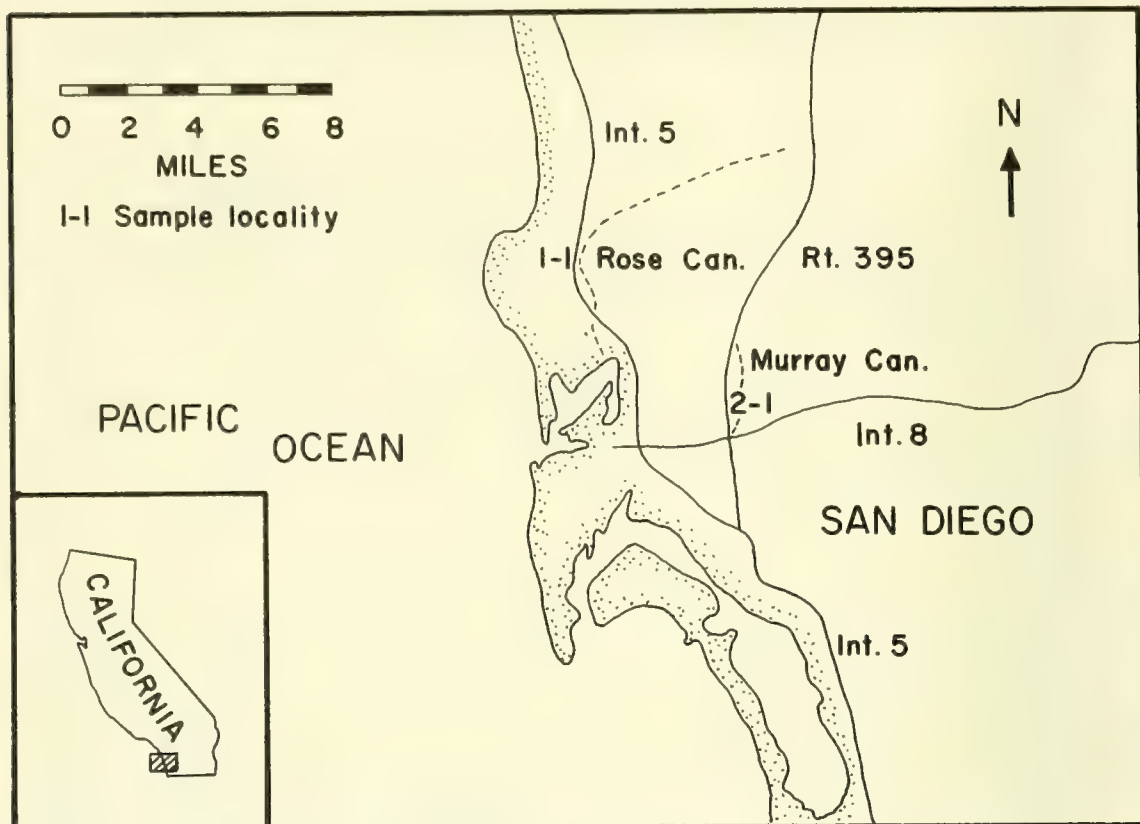


Figure 1. Map of San Diego Basin showing sample localities (see text for exact locations of sample sites).

ducted similar studies; they also found certain assemblages to be characteristic of distinct water depths. Bandy and Arnal (1960) used modern depth distributions of benthonic foraminiferal assemblages to interpret the paleoecology and paleobathymetry of Neogene deposits in the San Joaquin Basin, California.

The principles developed by Natland (1933), Bandy (1963a), and Bandy and Arnal (1957, 1960) are used herein to delineate the depositional site of the Eocene Ardath Shale and Stadium Conglomerate. Although the same species present in modern seas were not present during the Eocene, the general assemblages of modern forms when compared with like Eocene associations can be used to indicate the environs of deposition of the Eocene formations. The forms with the lowest depth ranges are used to determine the depositional site, so shoaler forms do not give erroneous results. Approximately 500 specimens were counted for each sample; percentages were computed on this basis.

Samples of the Ardath Shale were collected from the type locality in Rose Canyon behind the Rose Canyon Gas and Electric Company Power Sub-

station, which is located near the intersection of Ardath Road and interstate 5 (locality 1-1, Fig. 1). This suite of samples lies in the upper siltstone member of Milow and Ennis (1961) or the Ardath Shale of Kennedy and Moore (1971).

Stadium Conglomerate samples were collected in the Fenton Material Company Quarry in Murray Canyon, near the intersection of Friars and Murray Canyon Roads (locality 2-1, Fig. 1). Samples were collected from a megafossiliferous mudstone lens in the upper Poway Conglomerate unit of Milow and Ennis (1961) or the Stadium Conglomerate of Kennedy and Moore (1971).

LITHOSTRATIGRAPHY AND BIOSTRATIGRAPHY

The La Jolla group consists of tan-colored shales, sandstones, and mudstones with minor limestone and conglomerate. A southwestern source area for Ardath Shale sediments is suggested by Milow and Ennis (1961). Abundant molluscan and foraminiferid remains indicate a marine depositional site for the sediments.

TABLE 1. Dominant groups and species of foraminifera in samples of Ardath Shale and Stadium Conglomerate

STADIUM CONGLOMERATE		ARDATH SHALE	
GROUP/SPECIES	% TOTAL FAUNA*	GROUP/SPECIES	% TOTAL FAUNA*
Arenaceous	4	Arenaceous	13
<i>Gaudryina</i> sp.	1	<i>Cyclammina clarki</i> (Hanna)	5
Calcareous	98	<i>C. pacifica</i> Beck	1
<i>Anomalina affinis</i> (Reuss)	22	<i>Reophax curtus</i> Cushman	4
<i>A. coalingensis</i> Cushman and Hanna	1	<i>Textularia lajollaensis</i> Lalicker	1
<i>Bulimina</i> all sp.	1	Calcareous	78
<i>Cibicides sassei</i> Cole	9	<i>Anomalina regina minor</i> (Smith)	5
<i>Dentalina</i> all sp.	1	<i>Bolivina</i> all sp.	4
<i>Elphidium schencki</i> Cushman and			
Dusenbury	1	<i>Bulimina robertsi</i> Howe and Ellis	3
<i>Eponides dorfi</i> Toulmin	3	<i>B. schwageri</i> Yokoyama	12
<i>E. guaybalensis yeguaensis</i>	4	<i>Cibicides coalingensis minor</i> (Smith)	5
Weinzierl and Applin			
<i>Hanzawaia involuta</i> (Cushman		<i>Elphidium</i> sp.	1
and Dusenbury)	23	<i>Eponides dorfi</i> Toulmin	6
<i>Lagena</i> all sp.	1	<i>E. minima</i> Cushman	14
<i>Lenticulina</i> all sp.	1	<i>Gyroidina orbicularis planata</i> Cushman	20
<i>Melonis planatus</i> Cushman and			
Thomas	16	<i>Lenticulina</i> all sp.	1
<i>Nonion florinensis</i> Cole	1	<i>Marginulina hantkeni</i> Bandy	1
<i>Trifarina advena californica</i> Mallory	3	<i>Nodosaria</i> all sp.	2
Planktonic	1	Planktonic	9
Foraminifera/Ostracoda ratio	< 100	Foraminifera/Ostracoda ratio	> 100

*Ardath Shale percentages are the average of five samples from the same stratigraphic level; Stadium Conglomerate percentages are the average of four samples from the same horizon.

The genesis of the Poway group, including the Stadium Conglomerate, is discussed by Bellemin and Merriam (1958) and Woodford, Welday, and Merriam (1968). A provenance in the Coast Range Batholith is suggested by Woodford *et al.*, (1968). The Poway group consists of coarse sands and conglomerates with minor amounts of mudstone and siltstone. Marginal deposits yield terrestrial vertebrate and plant remains (Stock, 1937), while marine fossils (mollusks and foraminifera) occur in pebbly claystone lenses intercalated throughout the formation.

The Ardath Shale is characterized by a *Subbotina patagonica* (Todd and Knicker) planktonic foraminiferal fauna. The presence of *Truncorotaloides densus* (Cushman), *Pseudohastigerina micra* (Cole), *S. patagonica*, and *Truncorotaloides spinuloinflatus* (Bandy) brackets deposition between the base of the Middle Eocene and medial Middle Eocene according to the work of Bandy (1949), Bolli (1957, 1966), Pessagno (1961), Saito (1962), Jenkins (1965a, 1965b), Berggren (1968), and Samuel and Salaj (1968). The Ardath Shale planktonic foraminiferal fauna is equated with the *Globigerapsis*

kugleri-Hantkenina aragonensis interval of the standard zonation (Bolli, 1957) based on the age ranges of individual species.

A *Globorotaloides suteri* Bolli planktonic fauna characterizes the Stadium Conglomerate. The cooccurrence of *G. suteri* and *Truncorotaloides collacteus* (Finlay) suggests equivalence with the *Orbulinoides beckmanni* Zone of the standard zonation according to the work of Bolli (1957, 1966), Pessagno (1961), Saito (1962), Jenkins (1965a, 1965b), and Samuel and Salaj (1968). On this basis the Stadium Conglomerate is late Middle Eocene in age, not Upper Eocene as reported by Kennedy and Moore (1971).

BENTHONIC FORAMINIFERA

The Ardath Shale is characterized by a "Ulatisian" (*Amphimorphina californica* Zone) benthonic foraminiferal fauna (Mallory, 1959; Milow and Ennis, 1961), although several of Mallory's "Narizian" indices occur in the fauna (*Bolivina pisciformis* and *Anomalina regina minor*). The relative abundances of major foraminiferid groups and dominant benthonic species are listed in Table 1, and the complete

TABLE 2. Faunal reference list

ARDATH SHALE BENTHONIC SPECIES:

Ammopalmula sp.
Anomalina regina minor Smith, 1957
Bathysiphon eocenica Cushman and Hanna, 1927
Bolivina huxeri Howe, 1939
Bolivina pisciformis Galloway and Morrey, 1929
Bolivina sp.
Bulimina schwageri Yokoyama, 1890
Cibicides coalingensis minor (Smith) = *Cibicoides coalingensis minor* Smith, 1957
Cibicides praecursorius (Schwager) = *Discorbina praecursoria* Schwager, 1883
Cibicides sandiegensis Cushman and Hanna, 1927
Cyclammmina clarki (Hanna) = *Nonionina? clarki* Hanna, 1923
Cyclammmina pacifica Beck, 1943
Dentalina communis (d'Orbigny) = *Nodosaria communis* d'Orbigny, 1826
Elphidium sp.
Eponides dorfi Toulmin, 1941
Eponides minima Cushman, 1933
Fissurina sp.
Globulina sp.
Gyroidina orbicularis planata Cushman, 1935
Hormosina sp.
Karrerella elongata Mallory, 1959
Lenticulina antipoda (Stache) = *Robulina cultrata antipodum* Stache, 1865
Lenticulina inornata (d'Orbigny) = *Robulina inornata* d'Orbigny, 1846
Marginulina hantkeni Bandy, 1949
Nodosaria cocoaensis Cushman, 1925
Nodosaria latejugata Gumbel, 1868
Nodosaria parexilis Cushman and Stewart, 1930
Reophax curtus Cushman, 1920
Textularia lajollaensis Lalicker, 1935
Textularia sp.
Trochammina sp.
Vaginulinopsis mexicana nudicostata (Cushman and Hanna) = *Cristellaria mexicana nudicostata* Cushman and Hanna, 1927

STADIUM CONGLOMERATE BENTHONIC SPECIES:

Anomalina affinis (Reuss) = *Nonionina affinis* Reuss, 1851

Anomalina coalingensis Cushman and Hanna, 1927
Bulimina capitata Yokoyama, 1890
Bulimina schwageri Yokoyama, 1890
Buliminella sp.
Cibicides sassesi Cole, 1927
Dentalina capitata (Bouvignier) = *Nodosaria capitata* Bouvignier, 1852
Dentalina colei Cushman and Dusenbury, 1934
Dentalina consobrina d'Orbigny, 1846
Dentalina obliquistriata Reuss, 1851
Dentalina substrigata (Stache) = *Nodosaria substrigata* Stache, 1865
Dentalina vagina Stache, 1865
Ellipsonodosaria sp.
Elphidium californicum Cook, 1959
Elphidium schenki Cushman and Dusenbury, 1934
Eponides dorfi Toulmin, 1941
Eponides guaybalensis yeguaensis Weinzierl and Applin, 1929
Globulina landesi (Hanna and Hanna) = *Polymorphina landesi* Hanna and Hanna, 1924
Guttulina hantkeni Cushman and Ozawa, 1930
Hanzawaia involuta (Cushman and Dusenbury) = *Valvulineria involuta* Cushman and Dusenbury, 1934
Lagena becki Sullivan, 1962
Lagena conscripta Cushman and Barksdale, 1930
Lagena costata (Williamson) = *Entosolenia costata* Williamson, 1858
Lagena hexagona (Williamson) = *Lagena squamosa hexagona* Williamson, 1848
Lagena vulgaris Williamson, 1858
Lenticulina articulata texana (Cushman and Applin) = *Cristellaria articulata texana* Cushman and Applin, 1926
Lenticulina gyroscalpra (Stache) = *Cristellaria gyroscalprum* Stache, 1865
Lenticulina rotula (Stache) = *Cristellaria rotula* Stache, 1865
Melonis planatus (Cushman and Thomas) = *Nonion plantum* Cushman and Thomas, 1930
Nodosaria ewaldi Reuss, 1851
Nonion florinensis Cole, 1927
Trifarina advena californica Mallory, 1959
Uvigerina sp.

list of all species in Ardath Shale and Stadium Conglomerate samples are listed in Table 2. The presence of a substantial diverse arenaceous fauna characterized by abundant large *Cyclammmina* is suggestive of deposition in bathyal water depths according to Bandy and Arnal (1960) and Bandy and Kolpack (1963). Bandy (1963b) and Theyer (1971) determined the upper depth limit of *Cyclammmina* at 500 m. Size parameters of 50 specimens of *Cyclammmina* (1.8 mm in diameter) indicate water depths approximating 600 m (Theyer, 1971). The

foraminifera-ostracode ratio of greater than 100 suggests shelf or deeper water deposition (Bandy and Arnal, 1957). The lack of miliolids and the high percentage of planktonic foraminiferid tests both point to deep water deposition (Bandy and Arnal, 1960). Large percentages of species of *Eponides* in the samples represent shelf species displaced into deeper waters, possibly by turbidites. The association of species of *Anomalina*, *Gyroidina*, *Bulimina*, and *Cibicides* is strikingly similar to the abyssal biofacies (1500 m and deeper) of Bandy and

Arnal (1960). All factors seem to indicate an upper middle bathyal depositional site (600-1500 m) for the Ardath Shale.

The Stadium Conglomerate contains a "Narizian" benthonic foraminiferal assemblage. Dominant groups and species of Stadium Conglomerate foraminifers are listed in Table 1. Species of miliolids (reported from the Poway Conglomerate by Cushman and Dusenbury, 1934) associated with species of *Eponides*, *Cibicides*, *Nonion*, *Melonis*, *Anomalina*, and *Hanzawaia* point to a shelf depositional site for the Stadium Conglomerate according to work on modern distributions by Phleger and Parker (1951), Bandy and Arnal (1957, 1960), Olsson (1960, 1963), and Nogan (1964). No miliolids were present in the samples analyzed for this study. Low percentages of planktonic tests and the presence of non-ornamented buliminids is further evidence of shelf deposition (Bandy and Arnal, 1957). A site of deposition approximating 0-60 m is suggested for the Stadium Conglomerate.

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A SECOND RECENT SPECIES OF *NOETIA*, *SENSU STRICTO* (MOLLUSCA: BIVALVIA) IN THE TROPICAL EASTERN PACIFIC OCEANBARRY ROTH¹

ABSTRACT: Recent specimens of an arcoid bivalve differing in some particulars from *Noetia reversa* (Sowerby) are reported from Central American localities, and tentatively referred to *Noetia magna* MacNeil, described from the (?) Late Pliocene of Peru.

While sorting a suite of ark shells of the genus *Noetia* in the collection of the Geology Department, California Academy of Sciences, the author noted the presence of two distinct forms, the first being typical *Noetia reversa* (Sowerby, 1833), the second resembling the Late Pliocene or Pleistocene *Noetia magna* MacNeil, 1938, which bears considerably more and finer ribs on the exterior of the valves. An examination of all material in the collections showed the 2 forms to be present in lots from 2 other localities; and the distinction was also found to hold in material from the Natural History Museum of Los Angeles County and Stanford University. Because the existence in the Recent fauna of two such similar species cast doubt on the synonymy of *Noetia reversa* and *Noetia triangularis* Gray, 1857, (type species of the genus *Noetia*), a search was instituted for the type specimens of those 2 species.

Family Noetiidae

Genus *Noetia* Gray

Noetia Gray, 1840: 151 [*nomen nudum*]; Gray, 1857; MacNeil, 1938.

Type species, by original designation, *Noetia triangularis*, "n.s." Recent, no locality given [= *Arca reversa* (Gray MS) Sowerby, 1833; Recent, Tumbes, Peru].

Frizzell (1946) gave a critical discussion of factors affecting the suprageneric classification of arcoid pelecypods. MacNeil (1938) discussed the species of 8 genera and 1 subgenus which he placed in the subfamily "Noetinae." He gave the range of *Noetia* as "upper Eocene of the Indo-Pacific and . . . lower Miocene to Recent of America." Newell (1969) recognized 7 genera and subgenera in the subfamily Noetiinae and placed 3 subgenera under *Noetia*: *Eontia* MacNeil, 1938; *Incanopsis* Olsson, 1944 (= *Palestinarca* Vokes, 1946); and *Noetia sensu stricto*. He characterized the typical subgenus as follows: "Umbonal ridge carinate; radial ribs coarse, simple, not bifurcate over umbonal

slope; posterior margin subangular, commonly truncate."

For a discussion of the molluscan names published in the various editions of the "Synopsis of the Contents of the British Museum," in which *Noetia* appears as a *nomen nudum*, see Iredale (1913).

Noetia (Noetia) magna MacNeil

Arca (Noetia) reversa Gray, Grzybowski, 1899: 634-635, pl. 17, figs. 1, 1a [Not *Arca reversa* (Gray MS) Sowerby, 1833: 20].

(?) *Arca (Noetia) reversa* Sowerby, —subsp., Olsson, 1932; Miocene, Tumbes Formation, Zorritos, Peru.

Noetia magna MacNeil, 1938.

Noetia (Noetia) reversa magna [sic] MacNeil, Pilsbry and Olsson, 1941; Pliocene, Jama Formation, Ecuador; Pleistocene, Panama.

Noetia reversa magna [sic] MacNeil, Olsson, 1942a; Pliocene and Pleistocene, Burica Peninsula, Panama.

Type material: Holotype in Geological Institute of the Jagiellonian University, Krakow, Poland. Rubber cast of holotype, California Academy of Sciences, Department of Geology Type Collection No. 13630.

Type locality: Paita (Grzybowski). ?Late Pliocene, Mancora Tablazo Beds, Paita, Peru (*vide* Olsson, 1932).

Original description: According to MacNeil (1938: 38), "The form from Paita which Grzybowski referred to *Noetia reversa* is much like it in shape but differs in size, being about twice as large, and in having more ribs (40-42) as compared with 35 for *N. reversa*. Photographs of Grzybowski's specimens show it to have more elevated ribs, with less tendency to widen on the anterior part of the

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disk, although this might be a matter of individual variation. It compares with *N. reversa* in having strongly opisthogyrate, low, and very posterior beaks; these being at or even behind the posterior end of the cardinal area. The two species are extreme in this respect. Length 80 mm, height 72 mm, convexity 37 mm. The margins are eroded, so that only approximate measurements can be made."

DISCUSSION

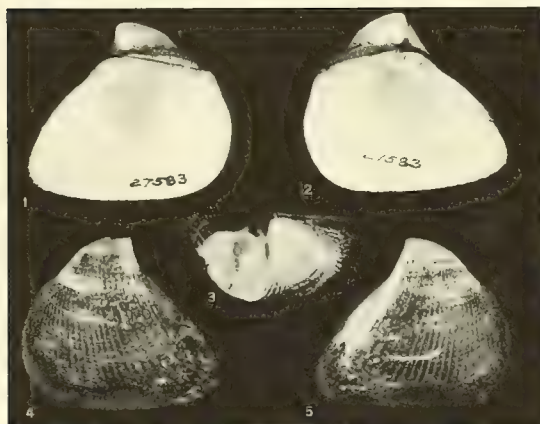
The existence of Recent specimens of *Noetia*, *s. s.* differing from typical *Noetia reversa* (Sowerby) was first noted by the author in a lot of beach valves from San Jose, Guatemala (Loc. 36678, CAS). Approximately 1 out of every 10 valves had between 42 and 47 radiating ribs; the remainder gave rib-counts of 31-37. Most authors have reported 35 or 36 as the number of ribs for *N. reversa*. [An apparent misprint in Olsson (1961) calls for 25 ribs].

Tabulation of rib-counts for all Recent *Noetia*, *s. s.* valves in the California Academy of Sciences, Natural History Museum of Los Angeles County, and Stanford University collections showed most falling between 31 and 37 (with 36 and 33 ribs most frequent), with another, smaller, concentration between 42 and 47. Counts of 38, 39, 40, and 41 ribs were obtained from only one valve each. The fine radiating sculpture of the extreme posterior dorsal portion near the beaks was excluded from the counting. This fine sculpture is difficult to detect on a shell with periostracum intact, and is the first feature to be eroded from beach specimens. Number of ribs is not directly correlated with shell size.

The results of the above tabulation seem to indicate the presence of two sympatric species. In

the California Academy of Sciences collection, fine-ribbed Recent specimens, resembling the holotype of *Noetia magna* MacNeil (1938), range from Corinto, Nicaragua (Loc. 27226, CAS) to near Mazatlan, Sinaloa, Mexico (Loc. 27583, CAS). The latter lot of 3 living specimens was trawled in 10-17 fathoms by the Templeton Crocker Expedition, July 29, 1932. One of the specimens is illustrated here (Figs. 1-5). The collection of the Natural History Museum of Los Angeles County contains a fine-ribbed example (LACM No. HH-756) from Venado Island, Panama Bay, Panama. It seems likely that future collecting and examination of other specimens will extend the known range even farther.

MacNeil (1938) distinguished *Noetia magna* from *N. reversa* on 3 characters: greater number of ribs in *N. magna*, tendency of the ribs to remain narrow anteriorly (which is really a function of their multiplicity), and the very large size of the shell. [MacNeil may have taken his measurements from a photograph. Dimensions of the plastotype (CAS No. 13630) match Grzybowski's measurements: length 75 mm, height 68 mm, convexity of one valve 34 mm]. Pilsbry and Olsson (1941) reaffirmed the size difference while placing *N. magna* as a subspecies of *N. reversa*. Recent specimens larger than about 60 mm in length parallel to the hinge line have not been seen by the author. The largest seen have even more ribs than the 40-42 described by MacNeil. The application of the name *N. magna* to the Recent species, therefore, may be regarded



Figures 1-5. *Noetia* cf. *N. magna* MacNeil. Hypotype (CAS No. 13675). Recent, off Mazatlan, Sinaloa, Mexico. Length parallel to hinge line 56 mm; height 52 mm.



Figures 6-10. *Noetia reversa* (Sowerby). Holotype of *Noetia triangularis* Gray, Reg. No. 1968856. Recent, locality unknown. Length parallel to hinge line about 34 mm; height about 30 mm. Photographs courtesy of and copyright by British Museum (Natural History).



Figures 11-15. *Noetia reserva* (Sowerby). "Possible syntypes" of *Arca reserva* Sowerby, BM (NH) (unnumbered). Recent. (?) Tumbes, Peru. Length parallel to hinge line about 40 mm; height about 33 mm. Photographs courtesy of and copyright by British Museum (Natural History).

as tentative. Olsson (1942a) reported that "the form [of *N. magna*] tends to be longer or more regularly rectangular," a statement which characterizes neither the holotype of *N. magna* nor most of the Recent specimens observed.

A list by Bosworth (1922) of mollusks from the tablazos of northern Peru, assigned by him to the Quaternary, consists entirely of species still living in the same general area. The Mancora Tablazo, presumed source of the type of *N. magna*, contains several extinct species as well, and was referred by Olsson (1942b) to the Late Pliocene.

The discovery that two similar species of *Noetia* occur in the Panamic province calls into question the synonymy, first advanced by Reinhart (1935), of *Noetia triangularis* Gray and *N. reversa* (Sowerby). Reinhart's study showed that *N. triangularis* is not a synonym of *Arca ponderosa* Say, 1822, as had been

assumed by some earlier workers. Photographs of the holotype of *N. triangularis*, B M (NH) Reg. No. 1968856, supplied by Dr. J. D. Taylor, British Museum (Natural History), and reproduced here (Figs. 6-10) show a shell with 36 major radial ribs and a few smaller, intercalary ribs on the posterior slope of the valve. No undoubted type specimen of *Arca reversa* Sowerby was located at the same institution, but photographs of a "possible syntype" supplied by Dr. Taylor (Figs. 11-15) show a specimen with approximately 33 major ribs. Both names, *Noetia triangularis* and *N. reversa*, would therefore seem to apply to the same species, the common large *Noetia* of the Panamic province, which is reported to range from Puertecitos in the northern Gulf of California to Mancora, Peru. Its apparent geologic range is Pleistocene to Recent.

Arca hemicardium Koch in Philippi (1843) was

described as having 20-22 ribs on the "posterior" (actually anterior) portion of the shell and 11-12 on the (posterior) slope. The accompanying figure shows a shell with about 38 ribs. Philippi (1844) himself synonymized *Arca hemicardium* and *Noetia reversa*, and many later authors have repeated the synonymy. Synonymies for *N. reversa* were given by MacNeil (1938) and Olsson (1961).

One interesting feature revealed by the present inquiry, as pointed out by Dr. Leo G. Hertlein, is that the relationship between *Noetia reversa* and *N. cf. N. magna* in the Recent fauna replicates a situation existing in the Miocene of Central America. Typical *Noetia macdonaldi* Dall, 1912, (type locality, Miocene, near Banana River, Costa Rica), common in the Gatun Formation and its equivalents in Costa Rica, Panama, and Colombia, has low beaks and wide anterior ribs. Occurring alongside it is a high-beaked form in which the anterior and posterior ribs are more uniform in size. Olsson (1922), believing Dall's type to be a high-beaked specimen, proposed the varietal name *subreversa* for the low-beaked form. MacNeil (1938) synonymized Olsson's name with that of Dall and proposed both *Noetia macdonaldi alta* for high-beaked shells from Costa Rica and *Noetia macdonaldi truncata* for Colombian specimens with very regular and comparatively narrow ribs. Whether the number and quality of ribs was more subject to individual variation in former times than at present, or if separate and sympatric species were involved remains to be shown by a statistical study. MacNeil also mentioned that specimens of *N. macdonaldi* average fewer and fewer ribs the higher one moves in the stratigraphic section at the type locality.

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For assistance during this investigation, the writer wishes to thank Leo G. Hertlein, Department of Geology, California Academy of Sciences; Myra Keen, Stanford University; James H. McLean and Gale Sphong, Natural History Museum of Los Angeles County; J. D. Taylor, British Museum (Natural History), who supplied excellent photographs of two specimens in question; W. Nowak, Geological Institute, Krakow; and M. Książkiewicz, Department of Geology, Jagiellonian University, Krakow, who furnished a cast of the holotype of *Noetia magna*.

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COVER: *The arborescent prickly pear cactus, Opuntia galapageia, growing on Bartholomew Island, one of the Galapagos group. This plant is believed to have evolved from a more shrubby, prostrate form in response to predation by lizards and the giant tortoise.*

*Photograph by C. F. Anderson,
Whitman College, Walla Walla,
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BULLETIN OF THE SOUTHERN CALIFORNIA
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EDITORIAL: A BIT OF HISTORY.¹

It is appropriate, as we begin a new volume, with new production arrangements and with responsibilities falling on new editorial officers, to summarize for our readers the history and accomplishments of the SCAS BULLETIN. The BULLETIN has been a significant medium for the reporting and communication of scientific information since the turn of the century. The first issues were published in 1902, eleven years after the Southern California Academy of Sciences was founded. Publication has been continuous in the ensuing seventy years and more than 1400 original contributions have been published. The BULLETIN also contains records of SCAS business and notices of interest to Academy members.

Contents of the BULLETIN have tended to reflect the professional interests and areas of productivity of the Academy membership. In the early years of publication, the majority of contributions in the biological sciences were botanical. A shift toward zoological papers occurred in the thirties, most of these being entomological. More recently there has been an increase in the number of contributions dealing with invertebrates other than insects and with vertebrate animals, and significant botanical papers also have been included.

Contributions in the physical sciences initially were mainly in chemistry and physics. A substantial increase in numbers of geological and paleontological papers occurred in the twenties and has continued until the present time. Most papers in the social sciences have been in the areas of anthropology and archeology. A detailed analysis of the contents of the first 60 volumes is available (Reish and Barnard, Index to the Bulletin of the Southern California Academy of Sciences, Vols. 1-60, 1966).

The Southern California Academy of Sciences currently is experiencing growth and diversification, both in membership and affiliated societies. As a result, recent annual meetings of the Academy have offered a rich variety of contributions in the natural and social sciences and the Academy has taken an increasingly active role in the

encouragement of young scholars in many disciplines. The BULLETIN is responsive to these changes and will continue to evolve according to the multidisciplinary interests of its contributors and readers.

It is a fact of history that the BULLETIN in its seventh decade is an effective and attractive organ of communication, drawing institutional strength from the Academy and its claim to excellence from the quality of individually contributed papers. That this is so today is due in large measure to the dedicated and effective service of two recently retired officers of the Academy. We owe much to Russell E. Belous, Treasurer of the Academy from 1964 to 1971 for sagacious management of Academy resources; for building the sound financial base upon which a viable BULLETIN depends. For high standards of quality, improved systems of manuscript review and evaluation, diversification of contents, and a modernized format we are in debt to Donald J. Reish, Editor of SCAS BULLETIN from 1967 to 1971. Our thanks to Don and Russ are an exception to the general disclaimer.¹ On this occasion we do record the appreciation of the Board of Directors and the entire Academy, as well as our own.

Finally, as shown by the history of the BULLETIN, a journal belongs not to its editors but rather to its readers and contributors. High professional standards and careful attention to the Instructions to Authors (inside back cover) on the part of contributors, and a demand for scholarly worth and clear communication on the part of readers will assure continued growth in usefulness and stature of the SCAS BULLETIN.

Patrick H. Wells, Technical Editor

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GENERIC PARTITIONING OF THE SOUTH AMERICAN LEPTODACTYLID
FROG GENUS *EUPSOPHUS* FITZINGER, 1843 (*SENSU LATO*)

JOHN D. LYNCH¹

ABSTRACT: The frog genus *Eupsophus* has been loosely defined and is heterogeneous. Study of osteological material revealed several major differences among the included species; these data when collated with published results of other workers on life history data and external morphology, provide the bases for definition and recognition of three genera of frogs now included in *Eupsophus* (*Eupsophus*, *Ischnocnema*, and *Thoropa*) and for placing some species in other genera (*Batrachyla* and *Niceforonia*). Owing to paucity of data, two species are not assigned to currently recognized genera (*Cystignathus sylvestris* and *Phrynopus peruanus*).

According to Gorham (1966) the leptodactylid frog genus *Eupsophus* contains 16 species (*E. bolitoglossus*, *E. columbianus*, *E. coppingeri*, *E. illotus*, *E. lutzi*, *E. miliaris*, *E. nodosus*, *E. peruanus*, *E. petropolitanus*, *E. quixensis*, *E. roseus*, *E. sylvestris*, *E. taeniatatus*, *E. versus*, *E. vertebralis*, and *E. wettsteini*). No author has dealt with the genus as a whole but reviews of several species groups are available (Bokermann, 1965; Cei, 1960, 1962; and Grandison, 1961). The limits of the genus have been debated by Bokermann (1965) and Gallardo (1965) who recommended removing three Brazilian species (*lutzi*, *miliaris*, and *petropolitanus*) from *Eupsophus* and using the genus *Thoropa* for these species. Gallardo (1970) and Barrio (1970) have generically isolated the species of Cei's (1960) and Grandison's (1961) *nodosus* group as *Alsodes* (including *coppingeri*, *illotus*, *nodosus*, and certain other names not mentioned in Gorham's list). Bokermann (1966) removed *bolitoglossus* from *Eupsophus* and considered the species identical with *Craspedoglossa sanctae-catharinae*.

Some other names have been allocated to *Eupsophus*. Rivero (1964) named *Eupsophus ginesi* from Venezuela; Lynch (1968a) allocated this species to *Eleutherodactylus* and tentatively assigned *columbianus* to *Niceforonia*. Lynch (1968a) placed *Syrrhophus juninensis* in the genus *Eupsophus*. Lynch (1968b) argued that *Alsodes monticola* Bell was an older name for the species Cei (1960, 1962) and Grandison (1961) called *Eupsophus coppingeri*.

The genus *Eupsophus* has been taxonomically difficult to define. Definitions employed by earlier authors have not been complete, in that the genus could not be separated from all others and because the extent of intrageneric variation

in some characteristics was not considered or known. In effect, *Eupsophus* was used for those leptodactylids not characterized by some distinctive features; evidence for the poor definition of the genus is provided by the submerged heterogeneity in osteological and life history data. *Eupsophus* was defined on the basis of narrow digital tips, absence of or very brief toe webbing, and pre-vomerine teeth lying between the choanae.

The purpose of this paper is to point out the heterogeneity of the species included in *Eupsophus* and to subdivide the genus into definable units. The 16 species included in the genus *Eupsophus* by Gorham (1966) belong to at least six genera; *Eupsophus* in the restricted sense would include only species from Argentina, Chile, and central Peru.

In the course of my generic review of the family (Lynch, 1971), I prepared skeletons of several species referred by various authors to *Eupsophus* and allied genera; study of the skeletal material and comparisons of the non-osteological traits of these species resulted in the conclusion that the generic arrangement of the frogs placed in *Eupsophus* and allied genera was in need of review. This impression is enhanced by Bogart's (1970) paper on the chromosomes of several species of the group.

Generic definitions of leptodactylid frogs are based on a number of osteological traits (arrangement of skull bones, shape of the vertebrae, and shape of the bones in the pectoral girdle), some myological traits (arrangement of the muscles of

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the hyoid, thigh muscles, and jaw muscles), external morphology, and larval traits (including egg size, deposition sites, and larval biology). Data for some traits are not available for all species but enough data are available to group the species and to comment on generic status.

METHODS

Specimens were made available from the collections of the American Museum of Natural History (AMNH), Field Museum of Natural History (FMNH), Kansas University Museum of Natural History (KU), Naturhistorisches Museum zu Wien, Vienna (NMW), University of Illinois Museum of Natural History (UIMNH), University of Michigan Museum of Zoology (UMMZ), United States National Museum (USNM), and Universitetes Zoologiske Museum, Copenhagen (ZMK). Preserved examples of the following species were examined (institutional abbreviations in parentheses indicate location of specimens): *Batrachyla leptopus* (KU, UMMZ), *Eupsophus juninensis* (KU, MCZ), *E. lutzi* (KU), *E. miliaris* (KU, UIMNH, UMMZ), *E. monticola* (FMNH), *E. nodosus* (FMNH, UMMZ), *E. peruanus* (UMMZ), *E. petropolitanus* (KU), *E. quixensis* (KU, UIMNH, UMMZ), *E. roseus* (FMNH, KU), *E. taeniatus* (KU, UMMZ), *E. versus* (ZMK), *E. wettsteini* (NMW), *Niceforonia festae* (KU, USNM), *N. flavomaculata* (KU, USNM), *N. montium* (MCZ), and *N. nana* (USNM).

Skeletal material in the form of dry, dermestid cleaned skeletons and cleared and stained preparations was used. The specimens used are listed elsewhere (Lynch, 1971); skeletons of the following species were studied: *Batrachyla leptopus*, *Eupsophus juninensis*, *E. lutzi*, *E. miliaris*, *E. petropolitanus*, *E. quixensis*, *E. roseus*, *E. taeniatus*, *E. wettsteini*, *Niceforonia festae*, *N. flavomaculata*, and *N. montium*. Superficial dissection was used to check certain cranial features (e.g., presence of quadratojugal, separation of nasal bones, presence of a frontoparietal fontanelle, and condition of the ear) in rare species (*Eupsophus monticola*, *E. nodosus*, *E. peruanus*, and *E. versus*).

Literature reports were used as data sources for external characteristics and breeding biology. My primary sources were Cei (1960, 1962), Gallardo (1962, 1970), Grandison (1961), and the original descriptions for species of which I saw no preserved examples—Barbour, 1922 (*illotus*), Tschudi, 1845 (*sylvestris*), and Grandison, 1961 (*vertebralis*).

CHARACTERISTICS OF GROUPS

Cei (1960, 1962) and Grandison (1961) defined three species groups of Chilean *Eupsophus* on the basis of position of the prevomerine teeth relative to the choanae, size of the omosternum, notching of the sternum, and exposure of the tympanum. Cei (1960, 1962) also commented on the other frogs sometimes included in *Eupsophus* and termed these the *peruanus-wettsteini* group (central Peru) and *Thoropa* (southeastern Brasil). Gallardo (1965) pointed out osteological bases for separating *Thoropa* from *Eupsophus* (shape of the terminal phalanges and arrangement of atlantal cotyles).

Before listing the characteristics of the species groups of frogs included in *Eupsophus* by various authors, it is germane to comment on the use of certain characteristics of the pectoral girdle in defining species groups of *Eupsophus*. All of the species included in *Eupsophus* have arciferal pectoral girdles, cartilaginous sterna, and an omosternum. Several authors have used the presence or absence of a posterior notch in the xiphisternum (= sternum here) to distinguish Argentine-Chilean species groups. The notch is present in the species of the *nodosus* group (all relatively large frogs) and absent in the species of the *roseus* and *taeniatus* group (smaller frogs). In species of the *miliaris* group, the large species (*miliaris*) has a notched sternum, whereas the smaller species have no notch in the sternum (*lutzi* and *petropolitanus*). I have not used this characteristic because it may simply be size-dependent and thus agree with a classification based on average adult size.

Three species (*lutzi*, *miliaris*, and *petropolitanus*) from the mountains of southeastern Brasil make up the *miliaris* group. This group is frequently recognized as the genus *Thoropa* (Bokermann, 1965; Gallardo, 1965) and is defined as follows: larvae aquatic, flattened and attenuate, labial papillae incomplete anteriorly; eggs large (5 mm in diameter in *lutzi*, Bokermann, 1965), pigmented; prevomerine dentigerous processes lying between choanae; tympana visible externally; fingers not bearing terminal pads, first finger equal in length to or shorter than second, males bearing spiny nuptial pads on thumb and sometimes second and third fingers; males lacking pectoral plates of spines; toes not bearing terminal pads, tips slightly expanded, lacking webbing, bearing slight lateral fringes; two metatarsal tubercles, inner much larger than outer; plantar surface lacking distinct supernumerary tubercles; quadratojugal bone pres-

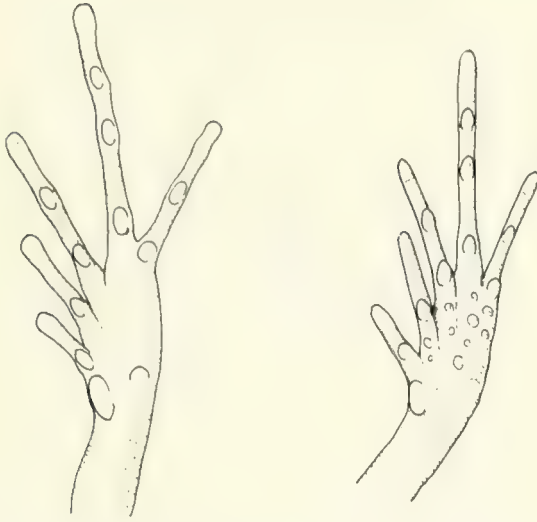


Figure 1. Plantar views of feet of *Thoropa miliaris* (left, KU 92852) and *Ischnocnema quixensis* (right, KU 99010).

ent; nasal bones separated; frontoparietal fontanelle present; occipital condyles widely separated; terminal phalanges T-shaped.

Three species (*illotus*, *monticola*, and *nodosus*) from western Argentina and central Chile make up the *nodosus* group (Cei, 1962; Gallardo, 1962). This group is defined as follows: larvae aquatic, not flattened or attenuate, labial papillae incomplete anteriorly; eggs large (3.2–3.6 mm in diameter), not pigmented (Cei, 1962; egg data only for *nodosus*); prevomerine teeth on processes lying between choanae; tympana not evident externally (lost in *monticola* and *illotus*); fingers not bearing terminal pads, first finger longer than second, males bearing nuptial asperities on thumb and second finger; males bearing pectoral plates of spines in breeding season (Cei, 1962; Gallardo, 1970); toes not bearing terminal pads, toes bearing indistinct to prominent lateral fringes and web rudiment (least developed in *nodosus*); two metatarsal tubercles, inner much larger than outer; plantar surface lacking distinct supernumerary tubercles; quadratojugal bone present; nasal bones separated (only *nodosus* studied); frontoparietal fontanelle present; occipital condyles narrowly separated; terminal phalanges knobbed.

Two species (*quixensis* and *versus*) are included in the *quixensis* group. One occurs in Amazonian Ecuador and Peru (*quixensis*) and the other is known from southeastern Brasil. This group is defined as follows: larvae not known, develop-

ment probably direct; eggs of *quixensis* are unpigmented and about 2.5 mm in diameter (ovarian eggs); prevomerine teeth on processes lying posteromedial to choanae; tympana visible externally; fingers not bearing terminal pads, first finger longer than second, males lacking nuptial asperities; no pectoral plates of spines; toes not bearing terminal pads, toes lacking lateral fringes and webbing; two metatarsal tubercles, equal in size; plantar surface bearing numerous conical supernumerary tubercles (Fig. 1); quadratojugal bone present; nasal bones in broad contact; no frontoparietal fontanelle; occipital condyles widely separated; terminal phalanges knobbed.

Two Chilean species (*roseus* and *vertebralis*) make up the *roseus* group here defined as follows: larvae not known; eggs large and unpigmented (Cei, 1962); prevomerine teeth on processes lying between or slightly posterior to choanae; tympana visible externally; fingers not bearing terminal pads, first finger shorter than or equal in length to second; males bearing nuptial asperities on thumb and second finger; no pectoral plates of spines; toes not bearing terminal pads, toes lacking lateral fringes and webbing; two metatarsal tubercles, inner much larger than outer; plantar surface lacking distinct supernumerary tubercles; quadratojugal bone present; nasal bones widely separated; frontoparietal fontanelle present; occipital condyles narrowly separated; terminal phalanges knobbed.

The Chilean *E. taeniatus* is distinctive compared to the other species and is included in its own group: larvae aquatic, not flattened or attenuate, labial papillae complete anteriorly (enclosing mouth); eggs large (3 mm in diameter) and pigmented (Cei, 1962); prevomerine teeth on processes lying between choanae; tympana visible externally; fingers not bearing terminal pads, first finger as long as second; males bearing nuptial asperities on thumb and second finger; no pectoral plates of spines; toes not bearing terminal pads, toes lacking lateral fringes and webbing; two metatarsal tubercles, inner much larger than outer; plantar surface lacking distinct supernumerary tubercles; quadratojugal bone absent; nasal bones widely separated; frontoparietal fontanelle present; occipital condyles widely separated; terminal phalanges T-shaped (comments to the contrary by Cei, 1960, 1962, and Grandison, 1961, are in error: dissection of the toe as a means of determining the shape of the terminal phalanges frequently results in breakage of the fragile lateral expansions).



Figure 2. Skulls of *Ischnocnema quixensis* (left, UIMNH 59643) and *Eupsophus roseus* (right, KU 84731).

The species from the plateau of central Peru are rare and poorly known. Four species are involved (*juninensis*, *peruanus*, *sylvestris*, and *wettsteini*). I have seen preserved examples of three (*sylvestris* is known only from lost type-material, *fide* Peters, 1873a) and have seen skeletons of *juninensis* and *wettsteini*. No reproductive data are available except that *juninensis* has large unpigmented eggs and none of the specimens known have nuptial asperities on the fingers or pectoral plates of spines. Prevomerine teeth are absent in *juninensis* and *wettsteini* but are present and lie between the choanae in the other two species. The tympana are visible externally in *peruanus*, *sylvestris*, and *wettsteini* but are lost in *juninensis*. The fingers and toes do not bear terminal pads and the first finger is shorter than the second. The toes lack lateral fringes and webbing; two metatarsal tubercles are present, the inner is larger in *juninensis* and *sylvestris*, but the tubercles are about of equal size in *peruanus* and *wettsteini*. Supernumerary plantar tubercles are absent in all four species. The quadratojugal bone is present in *juninensis*, *peruanus*, and *wettsteini*; the nasal bones are moderately separated in *juninensis* and *wettsteini*; *juninensis* has a small frontoparietal fontanelle, whereas *wettsteini* does not; the occipital condyles are narrowly separated in *juninensis* and widely separated in *wettsteini*; and the terminal phalanges are knobbed (*juninensis* and *wettsteini*). The species of this group are difficult to deal with because so much data are lacking. For

purposes of discussion this group is termed the *peruanus* group.

DISCUSSION

The six groups defined above are each homogeneous with the exception of the last group (*juninensis*, *peruanus*, *sylvestris*, and *wettsteini*). The major difficulty with that group is the paucity of specimens and information. On the basis of the group definitions each of the first five groups could be recognized as a distinct leptodactylid genus. The genus *Thoropa* is available for the *miliaris* group and is distinctive in tadpole morphology and osteology. In large measure, the genus has been recognized because the terminal phalanges are T-shaped (in contrast to the knobbed phalanges of the *nodosus* and *roseus* groups). Gallardo (1965) pointed out one skeletal feature which readily distinguishes the *miliaris* group (*Thoropa*) from the *nodosus* and *roseus* groups. In *Thoropa* the occipital condyles are widely separated and the atlantal cotyles are widely separated producing a gap at the occipito-cervical articulation, whereas in *Eupsophus* the condyles (and cotyles) are narrowly separated (Fig. 2) and there is no gap (Gallardo termed these two character states concave and convex atlas, respectively). Inclusion of the *miliaris* group in the genus *Eupsophus* greatly increases the limits of the genus and returns us to the era in which certain genera were taxonomic wastebaskets.

The *taeniatus* group (*taeniatus*) is distinctive in tadpole morphology and osteology (no quadratojugal bone, T-shaped terminal phalanges, and widely separated occipital condyles) when compared with the *nodosus* and *roseus* groups. The osteological data were not known to previous workers and thus the distinction of the group from other *Eupsophus* species was not appreciated. The definition of the group is identical with that for frogs of the genus *Batrachyla*. *Batrachyla* and *Eupsophus* have been separated on the basis of T-shaped terminal phalanges in the former by earlier authors (Cei, 1962) but are more distinctive than the single character difference usually cited. Loss of the quadratojugal bone is a frequent occurrence in some groups (e.g., Hylidae) but is uncommon among leptodactylid frogs (known only in *Crossodactylus*, *Batrachyla*, and *Eupsophus taeniatus*; Lynch, 1971). The widely separated occipital condyles in *Batrachyla* and *Eupsophus taeniatus* strongly contrast to the condition seen in the *nodosus* and *roseus* groups. Two solutions are available: (a) to include *Batrachyla* in the genus *Eupsophus*, or (b) to remove *taeniatus* from *Eupsophus* and include it as a species of *Batrachyla*. In order to maintain some homogeneity within leptodactylid genera, the latter choice is most preferable. Accordingly, *Eupsophus taeniatus* should be called *Batrachyla taeniata* (Girard), new combination. The definition of the genus *Batrachyla* is the same as that listed for the *taeniatus* group. As now constituted, the genus *Batrachyla* contains three species (*antartandica*, *leptopus*, and *taeniata*).

The *quixensis* group includes two species. The characteristics of the group require its removal from *Eupsophus*. Among the osteological features distinguishing this group from *Eupsophus* (*nodosus* and *roseus* groups) are the broad contact of the nasal bones, absence of a frontoparietal fontanelle, the more posterior position of the prevomerine dentigerous processes, and the round sacral diapophyses (slightly expanded in all other groups). The osteological features are unlike those found in *Batrachyla*, *Eupsophus*, *Hylorina*, *Telmatobius*, or *Thoropa* but are like those seen in advanced telmatobiine genera (*Eleutherodactylus* and allied genera). Inclusion of the species of the *quixensis* group in *Eupsophus* greatly increases the heterogeneity of the genus. In foot structure, the species of the *quixensis* group are distinctive from the other groups included in *Eupsophus*—no other groups have the large conical supernumerary plantar tubercles; the only argument for inclusion

of the *quixensis* group in *Eupsophus* rests on the simple digital tips (i.e., no pads) and ignores the other osteological data. The oldest generic name for the *quixensis* group is *Ischnocnema* Reinhardt and Lütken, 1862 (type-species *Leiuperus verrucosus* Reinhardt and Lütken). *Leiuperus verrucosus* Reinhardt and Lütken is an older specific name for *Eupsophus verrucosus* Miranda-Ribeiro, 1937, for which Gorham (1966) proposed a replacement name, *Eupsophus versus* (see systematic account).

I (Lynch, 1971) have previously argued that the genus *Eupsophus* (in the restricted sense) should be used for the species of the *nodosus* and *roseus* groups as well as part of the *peruanus* group. The species of the *nodosus* and *roseus* groups and *juninensis* (*peruanus* group) have narrowly separated occipital condyles (convex atlas of Gallardo, 1965), a quadratojugal bone, slightly dilated sacral diapophyses, knobbed terminal phalanges, separated nasal bones, and a frontoparietal fontanelle. The heterogeneity within and between these groups involves the secondary sex characteristics (pectoral plates of spines in males of the *nodosus* group but not in the *roseus* group or in *juninensis*) and external evidence of the ear (tympanic annulus and columella lost in *juninensis* and *monticola*, present but concealed beneath the skin in *illotus* and *nodosus*, and present and visible externally in *roseus* and *vertebralis*). On the basis of the concealed ear, basal webbing of the toe, presence of pectoral plates of spines in reproductive males, and the enlargement of the forearms in reproductive males, Gallardo (1970) proposed generic recognition of the *nodosus* group as *Alsodes*. He included a new species (*A. gargola*), some species usually included in *Telmatobius* (*montanus*, *prae-basalticus*, and *reverberii*), as well as the three *nodosus* group species (*illotus*, *monticola*, and *nodosus*) in the genus *Alsodes*. Barrio (1970) followed Gallardo in recognizing *Alsodes* but did not agree with the inclusion of *Telmatobius prae-basalticus* and *T. reverberii*. Gallardo's evidence for removing *montanus* from *Telmatobius* and placing it near *illotus*, *monticola*, and *nodosus* is compelling and appears to be the most correct disposition of *montanus* thus proposed. However, generic recognition of the *nodosus* group should be postponed because (1) the significance of ear reduction (or loss) is over-emphasized and does not consider the ear loss in *juninensis*, (2) while the pectoral plates of spines of the *nodosus* group are distinctive, the character state is duplicated to a lesser degree in some *Telmatobius* (*aemericus*,

hauthali, and *jelskii*), (3) the enlarged forearms in reproductive males of the *nodosus* group are no more distinctive than the condition seen in some *Leptodactylus*, and (4) the proper generic name for Gallardo's genus is *Hammatodactylus*, not *Alsodes*, if Fitzinger's (1843) work is older than Bell's (1843) as has been generally assumed.

The arguments in favor of recognizing the *nodosus* group as generically distinct from the *roseus* group depend in part on the lack of information concerning the species from the central plateau of Peru (*peruanus* group). Complete osteological data are available for only two Peruvian species (*juninensis* and *wettsteini*). One of these (*juninensis*) has the narrowly separated occipital condyles (convex atlas of Gallardo) like the Argentine-Chilean species (*nodosus* and *roseus* groups), whereas the other (*wettsteini*) has widely separated occipital condyles. Lynch (1968a, 1971) used *Niceforonia* for the Andean leptodactylids with widely separated occipital condyles, separated nasal bones, lacking a frontoparietal fontanelle, and having knobbed terminal phalanges. Stereoradiographs of paratypes of *Eupsophus wettsteini* reveal that osteologically this species is unlike *Eupsophus* and belongs to *Niceforonia*. Allocation of the other two species (*peruanus* and *sylvestris*) is not possible at present because data are lacking. The types of *sylvestris* are lost (Peters, 1873a) and no specimens matching the original description were found in Tschudi's Peruvian collections. Its inclusion in *Eupsophus* cannot be justified and in view of Peters' (1873a) comments *sylvestris* should be considered a *nomen dubium*. Peters' (1873b) *Phrynopus peruanus* may be a *Niceforonia* species; determination of its generic position must be postponed pending the availability of osteological material.

SYSTEMATIC ACCOUNTS

The following is a summary of the generic dispositions of the species included in *Eupsophus* by Gorham (1966) as well as other species referred to the genus by other authors but not included in Gorham's list. Each generic account includes a generic synonymy, definition, content, and when appropriate, remarks.

Batrachyla Bell, 1843

Batrachyla Bell, 1843:43 [Type-species by monotypy, *Batrachyla leptopus* Bell, 1843].

Definition.—see definition of *taeniatus* group.

Content.—Three species, *B. antartandica* Barrio, 1967, *B. leptopus* Bell, 1843, and *B. taeniata* (Girard) 1854. *Litoria glandulosa* Bell, 1843, is probably an earlier name for *Batrachyla taeniata* (see Cei, 1962).

Remarks.—Lynch (1971) pointed out that Boulenger's (1882) and Myers' (1962) combination of *Batrachyla* with *Eleutherodactylus* was in error.

Eupsophus Fitzinger, 1843

Eupsophus Fitzinger, 1843:31 [Type-species by original designation, *Cystignathus roseus* Duméril and Bibron, 1841].

Hammatodactylus Fitzinger, 1843:31 [Type-species by original designation, *Cystignathus nodosus* Duméril and Bibron, 1841].

Borborocoetes Bell, 1843:34 [Type-species by subsequent designation (Lynch, 1971), *Borborocoetes grayi* Bell, 1843. Preoccupied by *Borborocoetes* Schoenherr, 1842 (Insecta: Coleoptera)].

Alsodes Bell, 1843:41 [Type-species by monotypy, *Alsodes monticola* Bell, 1843].

Cacotus Günther, 1868:482 [Type-species by monotypy, *Cacotus maculatus* Günther, 1868].

?*Phrynopus* Peters, 1873:416 [Type-species by monotypy, *Phrynopus peruanus* Peters, 1873].

Borborocoetea Strand, 1928:55 [Replacement name for *Borborocoetes* Bell, 1843 (preoccupied); therefore taking the same type-species, *Borborocoetes grayi* Bell].

Definition.—larvae aquatic, not flattened or attenuate, labial papillae incomplete anteriorly; eggs large and unpigmented; prevomerine dentigerous processes situated between or slightly posterior to choanae or prevomerine dentigerous processes absent; tympana visible externally, concealed beneath skin, or lost; fingers and toes not bearing terminal pads; males with nuptial asperities on thumb and sometimes on chest; toes lacking webbing or having basal web; two metatarsal tubercles, inner much larger than outer; plantar surface lacking distinct supernumerary tubercles; quadratojugal bone present; nasal bones widely separated; frontoparietal fontanelle present; occipital condyles narrowly separated (convex atlas); terminal phalanges knobbed.

Content.—Eight species, *E. gargolus* (Gallardo), 1970, new combination, *E. illous* (Barbour), 1922, *E. juninensis* (Shreve), 1932, *E. montanus* (Lataste), 1902, new combination, *E. monticola* (Bell), 1843, *E. nodosus* (Duméril and Bibron), 1841, *E. roseus* (Duméril and Bibron), 1841, and *E. vertebralis* Grandison, 1961. Two other taxa may belong here but incomplete data preclude generic assignment: *Cystignathus sylvestris* Tschudi, 1845, and *Phrynopus peruanus* Peters, 1873.

Remarks.—Gallardo's (1970) recognition of *Alsodes* has not been followed here for the reasons cited in the discussion. Before the *nodosus* group



Figure 3. Dorsum, hand, and side of head of the holotype of *Leuiperus verrucosus* (ZMK 1180). (= *Ischnocnema verrucosa*).

is placed in a separate genus the relationships of the Patagonian *Telmatobius* must be more fully documented.

Ischnocnema Reinhardt and Lütken, 1862

Ischnocnema Reinhardt and Lütken, 1862:239 [Type-species by monotypy, *Leuiperus verrucosus* Reinhardt and Lütken, 1862].

Oreobates Jiménez de la Espada, 1872:87 [Type-species by monotypy, *Oreobates quixensis* Jiménez de la Espada, 1872].

Definition.—see definition of *quixensis* group.

Content.—Two species, *I. quixensis* and *I. verrucosa*; both species have acquired synonyms (see remarks).

Remarks.—The species of the genus bear considerable resemblance to some of the members of the genus *Eleutherodactylus* of southeastern Brasil (*binotatus*, *guentheri*, and *octavioi*). The terminal phalanges are knobbed in *Ischnocnema* and the tips of the digits lack expansions and the terminal transverse groove. In all *Eleutherodactylus* (including those of southeastern Brasil), there is a terminal transverse groove at each digital tip although there may be no digital expansion and the

terminal phalanges of some fingers knobbed. At present I am unwilling to place the two species of *Ischnocnema* in the genus *Eleutherodactylus*, although the possibility cannot be eliminated that the two species represent a single morphological divergence from the *binotatus* group of *Eleutherodactylus*.

Reinhardt and Lütken (1862) named a single specimen of a frog from Brasil as *Leuiperus verrucosus* in allusion to its warty skin (Fig. 3). In an appendix to their paper, the authors proposed the generic name *Ischnocnema*. They stated that they did so on the advice of Wilhelm Peters, who did not consider *verrucosus* to be a true *Leuiperus*. All subsequent authors, including Boulenger, Nieden, and Gorham, failed to notice this generic name. Apparently, the next author to examine the holotype of *Leuiperus verrucosus* was Cochran (1955), who, while retaining it in the genus *Pleurodema* (following Parker), noted that it bore considerable resemblance to the *Eleutherodactylus guentheri* group and little to *Physalaemus* or *Pleurodema*. Boulenger (1882) had placed the species in *Paludicola* and was uncritically followed by Nieden (1923). Parker (1927), without examining the unique holotype, placed it in *Pleurodema*. Much of the synonymy of the frog, as thus far presented, has resulted from its transferal within a complex of then poorly understood genera. The basis for the use of such names as *Leuiperus*, *Paludicola*, *Physalaemus*, and *Pleurodema* was not clarified until Parker (1927) pointed out the osteological bases for the recognition of *Physalaemus* and *Pleurodema* and the invalidity of *Paludicola* and *Leuiperus*.

The only synonyms of *Leuiperus verrucosus* of which I am aware are *Eupsophus verrucosus* Miranda-Ribeiro, 1937, and *Eupsophus versus* Gorham, 1966. Bokermann (1966) suggested that this species is an *Eleutherodactylus* but (*in litt.*) agrees that it is identical with Reinhardt and Lütken's specimen; Bokermann has directly compared the two holotypes.

Examination of the holotype of *Leuiperus verrucosus* conclusively demonstrates that the species is not a leptodactylid (since it lacks a bony style in the sternum) and therefore neither a *Physalaemus* nor a *Pleurodema*, both of which have prominent bony styles in their sterna. The absence of the terminal transverse groove at the digital tip and the knobbed rather than T-shaped terminal phalanges do not permit its association with *Eleutherodactylus*.

Gorham (1966), believing Miranda-Ribeiro's

name to be valid and correctly associated generically, proposed a replacement name, *Eupsophus versus*, since *verrucosus* is preoccupied in the genus *Eupsophus* by *Borborocoetes verrucosus* Philippi, 1902 (= *Eupsophus nodosus* Duméril and Bibron, 1841). Since it now appears that the Brazilian species is valid, a redescription of the type is presented below. Apparently only two specimens have been collected, each being the holotype of specific epithets of *verrucosus*.

Ischnocnema verrucosa (Reinhardt and Lütken).
1862

Leuiperus verrucosus Reinhardt and Lütken, 1862:171 [Holotype: Zoologiske Museum Kjøbenhavn (Copenhagen) 1180, from near Juiz de Fôra, Minas Gerais, Brasil].

Ischnocnema verrucosa: Reinhardt and Lütken, 1862:239.

Paludicola verrucosa: Boulenger, 1882:171; Nieden, 1923:507.

Pleurodema verrucosa: Parker, 1927:476; Cochran, 1955:355; Gorham, 1966:158.

Eupsophus verrucosus Miranda-Ribeiro, 1937:67, Fig. 1 [Holotype: Museu Nacional (Rio de Janeiro), from Rio Mutum, Coluna, Espírito Santo, Brasil, not examined].

Eleutherodactylus verrucosus [*verrucosus* of Miranda-Ribeiro, 1937, not Reinhardt and Lütken, 1862] (non *Hylodes verrucosus* Jiménez de la Espada, 1875): Bokermann, 1966:40.

Eupsophus versus Gorham, 1966:120 [Replacement name for *Eupsophus verrucosus* Miranda-Ribeiro, 1937; preoccupied in *Eupsophus* by *Borborocoetes verrucosus* Philippi, 1902 (= *Eupsophus nodosus* Duméril and Bibron, 1841)].

Redescription of holotype.—(Fig. 3). Snout subacuminate in dorsal view, rounded in lateral profile; lips not flared; canthus rostralis sharp, curved; loreal region concave; nostrils directed laterally, much closer to tip of snout than to eye; width of eyelid slightly greater than interorbital distance; interorbital region lacking bony ridges; tympanum small, higher than long, partially concealed, its diameter about 20% that of eye; maxilla and premaxilla toothed; prevomerine denticulous processes absent but the tissue of the prevomerine area badly damaged suggesting that denticulous processes probably were present originally [Miranda-Ribeiro (1937:67) recorded them present in his specimen]; choanae large, oval, situated laterally, completely visible when roof of mouth is viewed from directly above; tongue large, ovoid, posterior one-third free, not notched.

Skin of head, dorsum, flanks, and upper surfaces of limbs coarsely tuberculate; skin of venter and region about anus areolate; discoidal fold absent; fingers long and slender (Fig. 3) with prominent subarticular

tubercles; three palmar tubercles, outer smallest; supernumerary tubercles present on palm, few in number; tips of fingers not expanded and lacking any trace of terminal transverse grooves; tarsus lacking folds or tubercles on inner and outer edges; metatarsal tubercles large, subequal in size, inner oval, outer rounded, neither compressed; plantar supernumerary tubercles large, numerous; subarticular tubercles and tips of toes like those of hand.

Color.—Creamy-brown above spotted with darker brown; labial bars present, broad; venter dirty cream, chin with scattered pale cream spots; limbs barred creamy-brown and dark brown; posterior surface of thigh uniform bleached cream; dark brown anal patch.

Measurements in mm.—Snout-vent length 22.1; tibia 12.0; head width 9.3; head length 8.5; tympanum length 0.65; eye length 3.2; interorbital distance 2.3; eyelid width 2.3+.

Variation.—The specimen described and figured by Miranda-Ribeiro (1937) had more clearly defined markings dorsally and the light spots on the throat and flanks were better defined. These differences probably best reflect the length of time the holotype of *Leuiperus verrucosus* has been preserved. Miranda-Ribeiro reported the tympanum to be 40% the diameter of the eye in his specimen, whereas the tympanum/eye value in the holotype of *L. verrucosus* is 0.203. This difference may reflect differences in measuring techniques and/or variation. An index of variation is obtained by examining the same statistic in the only congener, *Ischnocnema quixensis*; in 24 adult and subadult specimens (sexes pooled) the values have a range of 0.48–0.66 and a mean of 0.589.

Ischnocnema quixensis has at least three synonyms. *Hylodes philippi* Jiménez de la Espada, 1875, and *H. verrucosus* Jiménez de la Espada, 1875, are considered synonyms (Lynch and Schwartz, 1972) and *Leptodactylus tuberculosus* Anderson, 1945, is here added to the synonymy. W. Ronald Heyer and I have examined the holotype. The absence of a bony style in the sternum requires removal of *tuberculosus* from *Leptodactylus*. The presence of conical plantar supernumerary tubercles, two large metatarsal tubercles, smooth skin of the venter, tuberculate skin of the dorsum, long first finger, and absence of discoidal folds and absence of digital expansion characterize *Ischnocnema*; the size, color pattern, and large and prominent tympanum characterize *I. quixensis*.

Thoropa Cope, 1865

Thoropa Cope, 1865:113 [Type-species by monotypy, *Cystignathus missiessii* Eydoux and Souleyet, 1841].

Definition.—see definition of *miliaris* group.

Content.—Three species, *T. lutzi* Cochran, 1938, *T. miliaris* (Spix), 1824, *T. petropolitana* (Wandolleck), 1907.

Remarks.—Excellent accounts of the species of this genus are available in the works of Bokermann (1965) and Cochran (1955). *Ololygon* Fitzinger is frequently cited as a synonym, whereas in fact the generic name *Ololygon* was proposed in 1843 for *Hyla strigilata* Spix and is therefore a synonym of *Hyla*.

The species included in *Eupsophus* by Gorham (1966) but not allocated to *Batrachyla*, *Eupsophus*, *Ischnocnema*, or *Thoropa* here are listed below with their taxonomic disposition.

Borborocoetes bolitoglossus Werner, 1897, is presently considered a synonym of *Craspedoglossa sanctaecatherinae* (Bokermann, 1966).

Borborocoetes columbianus Werner, 1899, is presently included in the genus *Niceforonia* (Lynch, 1968a).

Cystignathus sylvestris Tschudi, 1845, is so poorly known (Peters, 1873a) that it should be considered a *nomen dubium*.

Eupsophus wettsteini Parker, 1932, is here considered a species of *Niceforonia*.

Phrynopus peruanus Peters, 1873, cannot be assigned to genus with the available data. It is either a species of *Eupsophus* or of the generic group now called *Niceforonia*; that decision must be postponed pending acquisition of more material.

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FIRST RECORD OF THE BLACK SCABBARDFISH, *APHANOPUS CARBO*,
FROM THE PACIFIC OCEAN WITH NOTES ON OTHER
CALIFORNIAN TRICHIURID FISHES

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ABSTRACT: Based upon three specimens collected in the vicinity of Fort Bragg, California, *Aphanopus carbo* Lowe, 1839, is reported from the Pacific Ocean for the first time. Data and keys are presented for distinguishing *A. carbo* and four other species of Californian trichiurids (*Assurger anzac*, *Diplospinus multistriatus*, *Lepidopus xantusi*, and *Trichiurus nitens*). Key characters include shape of caudal fin, shape of dorsal fin, presence or absence of ventral fins, body depth into standard length, and counts of dorsal rays, anal rays, vertebrae, and pyloric caeca. Otoliths (sagittae) of the five species are illustrated and differentiated on the basis of shape, proportions, and size.

Although the black scabbardfish is relatively common in the eastern north Atlantic (Tucker, 1956; Sutro, 1967; Forster, 1971), only three individuals have been noted from the western north Atlantic (Templeman and Squires, 1963), and until now only one specimen, from the Gulf of Aden (Norman, 1939), has been recorded outside the Atlantic Ocean.

On March 18, 1969, a black scabbardfish (*Aphanopus carbo*) was taken in an otter trawl being fished from the vessel *Pearl Harbor* in 270 fathoms (494 m) of water off Bodega Bay, California. This fish, a female, 1038 mm total length (TL) and weighing 1950 g (Table 1), was turned over to the California Department of Fish and Game by Kenny Marsh, skipper of the *Pearl Harbor*. Eight months later a smaller individual was trawled in 300 fathoms (549 m) west of Fort Bragg by the vessel *Northern Light*, skippered by Angelo Urbani. A third specimen was netted on February 16, 1971, by Tom Webster, skipper of the otter trawler *Havana*, while fishing in 360 to 390 fathoms (658–713 m) approximately 20 miles (32 km) west of Bodega Bay. As nearly as we can determine, these are the first and only captures of *A. carbo* in the Pacific Ocean; all three specimens have been placed in the fish collections of the Natural History Museum of Los Angeles County.

Tucker (1956) examined the holotypes of several nominal species of *Aphanopus* and determined that none could be distinguished from the earliest described species, *A. carbo*. Templeman and Squires (1963) compared morphometrics for their three western Atlantic specimens with Tucker's data, and aside from having a slightly

greater number of vertebrae (100–103 vs. 98–99) in the western Atlantic fish, there were no obvious differences. The three fish from off California have an even higher number of vertebrae (105) and inasmuch as it does not appear that Tucker (1956) checked vertebrae on more than three individuals, we asked G. E. Maul (Museu Municipal do Funchal, Madeira) to send us vertebral counts on additional Madeiran material. He was able to obtain counts on 16 individuals as follows [number of individuals (precaudal + caudal including hypural = total)]: 1(40+59=99), 2(41+57=98), 3(41+58=99), 3(42+57=99), 3(42+58=100), 1(42+59=101), 1(42+60=102), 1(43+57=100), 1(43+58=101). Total vertebrae (105) for the Californian *Aphanopus* (Table 1) thus exceed the highest Atlantic count (103), but one of the western Atlantic specimens (Templeman and Squires, 1963) matched our 46 precaudal vertebrae, and three of the fish examined by Maul (data above) had caudal vertebral counts (59 and 60) that were equal to or exceeded those of the Californian specimens. For this reason, we believe that the apparent difference in total vertebrae merely reflects the effect of colder temperatures on the developing egg, and would be resolved upon examination of additional material from higher latitudes in the north Atlantic (e.g., Newfoundland, Greenland, Iceland). This hypothesis assumes of course that the eggs of *Aphanopus* are pelagic and develop in the upper surface layers.

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TABLE 1. Selected morphometric and meristic data on three species of Californian trichuriids (standard lengths in mm, all other measurements expressed as thousandths of SL.)

Measurements	<i>Aphanopus carbo</i>			<i>Assurger anzac</i>		<i>Lepidionotus xantusi</i>				
Standard length	955	965	990	1534	1612	180	375	473	688	705 850
Head length	187	196	190	074	080	182	209	211	231	207 240
Fleshy orbit	034	030	033	010	010	030	036	033	040	038 064
Bony interorbital	031	032	029	008	009	022-029	024	027	023	02
Snout length	075	080	074	028	032	060-069	070-076	071	082	
Maxillary length	089	089	088	024	024	058-072	072-079	074	084	
Pectoral length	090	087	093	031	-	084-100	091-097	083	099	
Snout to D, insert	155	165	158	050	056	126-147	145-157	145-162		
Snout to P, insert	196	200	190	085	072	186-206	203-223	199-226		
Snout to A, insert	576	580	586	391	422	529-570	552-560	539-584		
Snout to V, insert	200	195	184	108	111	216-228	226-247	229-252		
Depth	090	099	098	037	039	075-096	097-114	094-121		
P to D, insert	069	072	069	044	045	082-090	089-102	089-102		
V to D, insert	092	093	088	070	068	117-135	131-143	131-146		
Counts:										
Dorsal rays	XLIII,55	XLIII,54	XLII,55	116	117	78-81				
Anal rays	II,47	II,47	II,48	II,74	II,76	II,42-47				
Pectoral rays	12	12	12	12	12	12				
Gill rakers	-	-	-	4+9	4+9	6-8+10-13=16-21				
Vertebrae	-	46+59=105	46+59=105	-	43+84=127	32-36+48-55=84-87				
Pyloric caeca	7	7	7	-	13	16				
No. of specimens	1	1	1	1	1	10	3	12		

* Measurements of *L. xantusi* are presented by size groups to reveal allometric growth, if present.

Based upon catch data for 15 specimens of *Aphanopus carbo* taken on longline gear in the Biscay area, Forster (1971) suggested that its distribution is determined by temperature rather than depth. Twelve of these 15 specimens were studied by Bone (1971) and were the basis for his report on the behavior, histology, and anatomy of *A. carbo*. It was his view that ambient light is more important in determining the distribution of *A. carbo* than either temperature or depth.

In an excellent narrative of the commercial fishery off the island of Madeira, Sutro (1967) presents a few details regarding the life history of the "black espada." He points out that at one time a 4-foot (122 cm) long black scabbardfish would sell for five cents (about one cent a pound), but it is now Madeira's most popular fish, often selling for 30 cents a pound. A typical fishing boat carries a crew of four, and utilizes four lines. Each line averages about 4600 feet (1402 m) long and is fished vertically with the hooks spaced 10 feet (3 m) apart on the lowermost 1400 feet (427 m) of the line. Although the number of fish captured in one night varies considerably, a good catch would be about 100 black scabbardfish.

OTHER CALIFORNIAN TRICHIURIDS

Assurger anzac (Alexander, 1916)

Radovich (1961) noted a razorback scabbardfish caught on May 3, 1958, off the north point of North Coronado Island, and mentioned that the species previously had been taken off California in 1951. The specimen from North Coronado Island (Scripps Institution of Oceanography collection number SIO 58-75) apparently had been snagged, as it bears hook marks near the origin of the anal fin; this fish measured 1035 mm standard length (SL) and 1054 mm total length (TL). The specimen caught in 1951 measured 1640 mm TL and was taken on September 23, presumably on hook and line, in the surf at Playa del Rey. This fish is deposited in the collection of Scripps Institution of Oceanography, La Jolla (SIO 58-80).

Since Radovich's report, two additional specimens of *Assurger anzac* have been taken in Californian waters. One of these, a female measuring 1534 mm SL, weighing 555 g (Table 1), was snagged on January 1, 1963, by two fishermen, Joe Branin and Guy R. Ludwick, approximately

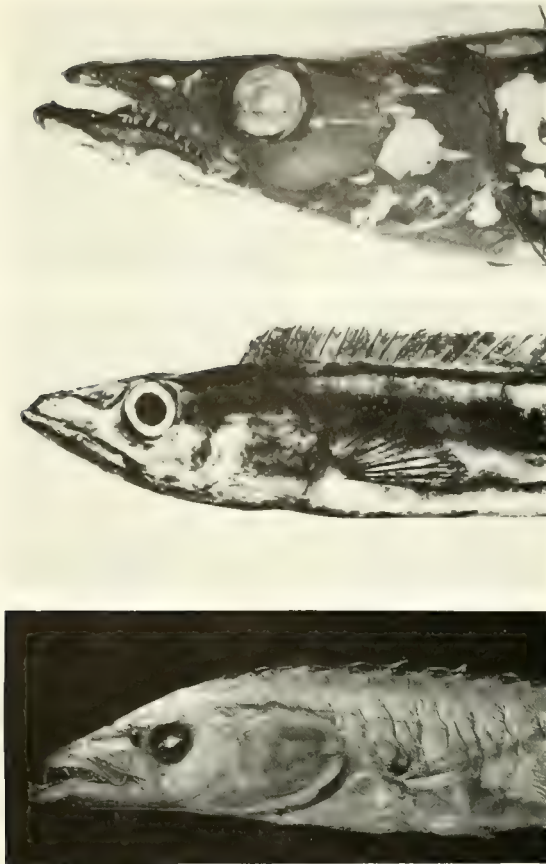


Figure 1. Comparison of head and trunk region of three adult Californian trichiurids: *Aphanopus carbo* (top), *Lepidopus xantusi* (center), *Assurger anzac* (bottom).

1½ miles (2.4 km) off Laguna Beach. This specimen was deposited in the fish collection at the University of California, Los Angeles. The most recently collected individual was picked up by Mike McGiffin as it was feebly floundering in the surf at Torrance Beach, Santa Monica Bay in 1965. The entire posterior extremity of this fish was missing from a point just behind the anal fin insertion (possibly 55% of the length of the fish), apparently the result of a shark bite, which may also account for its being in the surf. The standard length of this fish may have been between 1700 and 1800 mm judged by its measurable length.

Due to the rarity of *Assurger anzac* the following description is presented. The body color, when fresh, is an overall silver that is easily rubbed off. The dorsal fin membrane is black between the first and third fin spines as is the base of the membrane between spines three and four; the remainder of

the dorsal fin membrane is unpigmented. There is one row of sharply pointed teeth along the lower jaw that are slightly curved inward and are about twice as strong as those in the upper jaw. There are one or two lanceolate teeth at the tip of the lower jaw that are two to three times as long as the other teeth. Two or three teeth, which are firmly fixed at the tip of each premaxillary, are similar in size to the large lanceolate teeth in the lower jaw.

Each primary gill raker consists of one to three bristle-like spines on a slightly raised basal plate. Secondary rakers, consisting of fewer and shorter bristles on smaller plates, are interspersed with the primary rakers. Secondary and rudimentary rakers extend to the extremities of both the upper and lower limb of the first gill arch.

At a level directly above the pectoral insertion, the lateral line lies approximately one-third of the distance between the dorsal and ventral profiles; it descends from there in a straight line, reaching the mid-side about two head lengths behind the pectoral, then runs parallel to the body axis (horizontally) until it terminates on the caudal peduncle.

We did not differentiate spines and rays in the dorsal fin and counted vertebrae on only one specimen (Table 1). The first 63 to 65 anal rays are small, prostrate (lie parallel to the body) and embedded.

In addition to the Californian specimens, two smaller individuals from the stomachs of *Alepi-saurus* were examined. These two trichiurids are deposited in the Scripps Institution of Oceanography collections; one measures 760 mm SL and was taken off the coast of Chile (lat. 26°04.9' S, long. 101°47.0' W), the other is a much smaller, badly mangled, fish from northeast of Midway Island. The Chilean specimen had 119 dorsal fin rays, but the elements in the anal fin could not be counted.

The stomach of the fish from North Coronado Island contained a small squid and an anchovy, *Engraulis mordax*; whereas there were beaks from three cephalopods in the stomach of the *Assurger* from off Laguna Beach. An incomplete vertebral column from a small Pacific hake, *Merluccius productus*, was found in the stomach of the specimen taken at Torrance Beach in 1965.

Diplospinus multistriatus Maul, 1948

In August, 1957, a commercial fisherman obtained a four-inch long trichiurid that had been

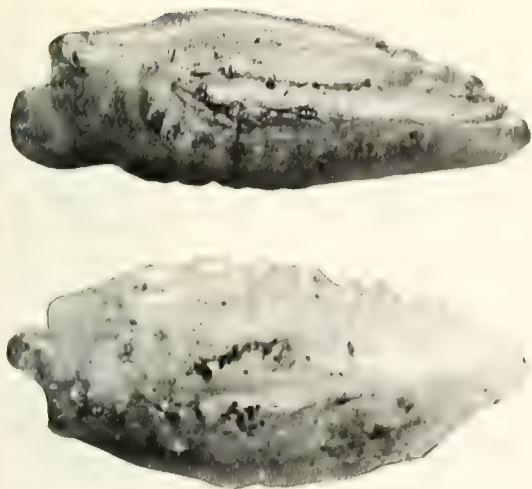


Figure 2. Left sagittae of *Diplospinus multistriatus* 4.2 mm (top) and *Paradiplospinus gracilis* 2.7 mm (bottom). Photos by Jack W. Schott.

regurgitated by an albacore which he caught 250 miles southwest of Morro Bay (lat. $33^{\circ}10'N$, long. $125^{\circ}10'W$). The spinous and soft-rayed portions of the dorsal fin were completely separated; the soft-rays were much more crowded than the spines. This trichiurid appeared to be conspecific with *Lepidopus gracilis* described by Brauer (1906) from the west coast of Africa. However, Bussing (1965) assigned Brauer's fish to *Paradiplospinus* and presented data to distinguish it from *Diplospinus multistriatus*. Judged by Bussing's data, our specimen should be assigned to *D. multistriatus*, but various counts made on 12 additional specimens found in stomachs of *Alepisaurus* indicate the differences between *P. gracilis* and *D. multistriatus* are not as distinct as Bussing shows. Although the otoliths offer additional proof that *P. gracilis* and *D. multistriatus* are not conspecific, the observed differences in the sagittae of these two taxa appear to be of specific rather than generic magnitude (Fig. 2).

Andriashev (1960), in establishing *Paradiplospinus*, distinguished it from *Diplospinus* on the basis of a number of substantial characters which do not permit both species to be assigned to the same genus. Unfortunately, he did not have comparative material of *Diplospinus*, and he relied entirely upon published data. Two of his substantial characters were not discussed in the publications he consulted, and the variation he attributed to *Diplospinus* in these instances may not have been based upon fact. Some of his other

characters should have been deemed "relative" rather than "substantial." In fact, it appears that Bussing (1965) had reservations regarding the validity of *Paradiplospinus* in his statement "the discovery of ventral fins in small specimens of *P. gracilis* does not invalidate the genus *Paradiplospinus*, although several characters suggest its similarity with *Diplospinus*." To the characters noticed by Bussing we can now add the otoliths (sagittae).

Ahlstrom (1971) records larval *Diplospinus multistriatus* from numerous eastern Pacific localities, both north and south of the equator, and recently informed one of us (Fitch) that he has seen fair numbers of larval *D. multistriatus* off southern California; some within 200 miles (320 km) of the coast. During several tuna longline cruises in 1954 and 1955, the California Department of Fish and Game research vessel *N. B. Scofield* caught a number of *Alepisaurus ferox* that had eaten juvenile *Diplospinus*. In all, 65 specimens, ranging from just over two to about four inches (50–100 mm) in length, were recovered from the stomachs of *Alepisaurus*. These fish were taken primarily within the area bounded by lat. 24° and $35^{\circ}N$, and long. 124° and $137^{\circ}W$. The stomachs of two small individuals of *Alepisaurus* which had been eaten by a larger *Alepisaurus* caught on longline gear (lat. $24^{\circ}03'N$, long. $137^{\circ}12'W$) on January 27, 1954, contained 53 of the 65 juvenile *Diplospinus multistriatus* examined by us. Twelve of these two- to three-inch (50 to 75 mm) long fish were cleared and stained and yielded the following counts (number of individuals noted in parentheses for each count): dorsal spines, 30(1), 32(1), 33(7), 34(3); dorsal rays, 35(1), 36(2), 37(3), 38(1), 40(1); anal rays, 26(1), 28(1), 29(1), 30(1), 33(1); pre-caudal vertebrae, 24(4), 25(6), 27(2); total vertebrae, 59(1), 60(7), 61(4). There are two anal spines, one pelvic spine with no rays, 12 pectoral rays, and $9 + 8$ principal caudal rays.

Diplospinus multistriatus previously has not been reported from off California, and does not appear in the checklist of deep-water fishes given in Fitch and Lavenberg (1968). Because of their extremely small sizes and generally poor condition, none of the specimens we examined from the eastern north Pacific was photographed.

Lepidopus xantusi Goode and Bean, 1895

Tucker (1956) reported that the earliest descriptions of *Lepidopus xantusi* are misleading.

and confusing, yet there is no doubt but what the name was applied to a specimen from off Cape San Lucas, Baja California. Because of erroneous reports, Tucker (1956) stated that "a new name will have to be found for it by the first worker able to re-describe it from material." However, Jordan and Starks (1907) described fully and illustrated a 2½-foot (76 cm) long *L. xantusi* collected by C. F. Holder at Santa Catalina Island, California. In view of this accurate description, in addition to the fact that only one species of *Lepidopus* is known to exist in the eastern north Pacific, we prefer to retain the name *L. xantusi* for this species.

Lepidopus xantusi has been called "black scabbardfish" in California (Fitch and Lavenberg, 1968) and "scabbardfish" by the American Fisheries Society (Bailey et al., 1970). Inasmuch as *Aphanopus carbo* has historically been known as the black scabbardfish, we propose the vernacular name "Pacific scabbardfish" for *L. xantusi*. This will circumvent confusion and name changing should the closely related Atlantic species *L. caudatus* ever be found to occur within the area covered by the American Fisheries Society.

The distribution of *L. xantusi* extends from Eureka, California, to Mazatlan, Mexico (Fitch and Lavenberg, 1968). The silver-colored juveniles up to 12 inches (30 cm) long apparently live near the surface and often stray into relatively shallow water near shore. The adults, however, have always been captured in deep water. Those caught on hook and line have been taken from 350 to 1650 feet (107 to 503 m) beneath the surface, usually at or near the bottom. The largest measured individual was 900 mm TL (Table 1), although unpublished records from the California Department of Fish and Game show an individual 102 cm TL that was caught "in 275 fathoms south of Santa Catalina Island on November 16, 1938." Maximum observed weight was 1120 g for a ripe male 835 mm TL.

The otoliths of numerous individuals were examined for evidence of age and from this investigation it appears that a specimen 375–400 mm TL, weighing 70 to 85 g, is approximately 4–5 years old. Individuals measuring 830–888 mm TL (770–1070 g) have 15–18 winter annuli on their otoliths.

Although most captures of *L. xantusi* have involved but one fish, in April 1962, a commercial fisherman caught 1½ tons (1360 kg) of these fish in an otter trawl being towed on the bottom in 140 fathoms (256 m) off Newport Beach, California.

On another occasion, a sport fisherman caught five large adults while fishing near the bottom in very deep water (± 300 m) near San Diego. Apparently, *L. xantusi* is a schooling fish at times.

During the past 25 years, we have examined more than 50 individuals ranging in standard length from 47 to 850 mm, however, we have included counts and morphometrics for only 25 of these in this report (Table 1). These specimens cover the entire range of variation which we observed in *L. xantusi* for the sizes indicated.

Two badly digested specimens of *Lepidopus*, removed from the stomach of a yellowfin tuna (*Thunnus albacares*) captured 28 miles (45 km) northwest of Zorritos, Peru (lat. 03°22' S, long. 81°01' W), probably represent an undescribed species and are not included in this account. These specimens (deposited in the UCLA fish collection) have slightly higher dorsal and anal fin counts than any *L. xantusi* we have examined. Furthermore, there are other observable differences in spite of their poor condition. A satisfactory description of this Peruvian *Lepidopus* must await the collection of less wretched material.

Trichiurus nitens Garman, 1899

The Pacific cutlassfish has been recorded from a number of localities between San Pedro, California, and Paita, Peru, but they were taken in commercial quantities only during the early 1930's. Typically, one or two individuals are caught within a period of hours or days, then several years pass before the species again appears. However, during the early 1930's, small lampara boats fishing in relatively shallow water near San Pedro, Long Beach, and Seal Beach were capturing from a few pounds to a ton or more almost daily for short periods each spring.

The largest specimen that we have observed was a 44-inch (112 cm) long female netted in March, 1962, that weighed approximately 3¼ pounds (1460 g). This fish was 7 years old, judged by the growth rings on its otoliths, and was approaching the onset of spawning. A 33-inch (83 cm) male taken a month earlier was 4 years old and appeared to have viable milt in its testes.

Hubbs and Hubbs (1941) pointed out numerous characters by which *T. nitens* can be distinguished from the Atlantic *T. lepturus*. However, Tucker (1956), felt that "the satisfactory establishment of *T. nitens* requires, not comparison with Atlantic material, but demonstration of a non-cline discontinuity across the Pacific." Since we lack ma-

OTOLETHS OF CALIFORNIAN TRICHIURIDS

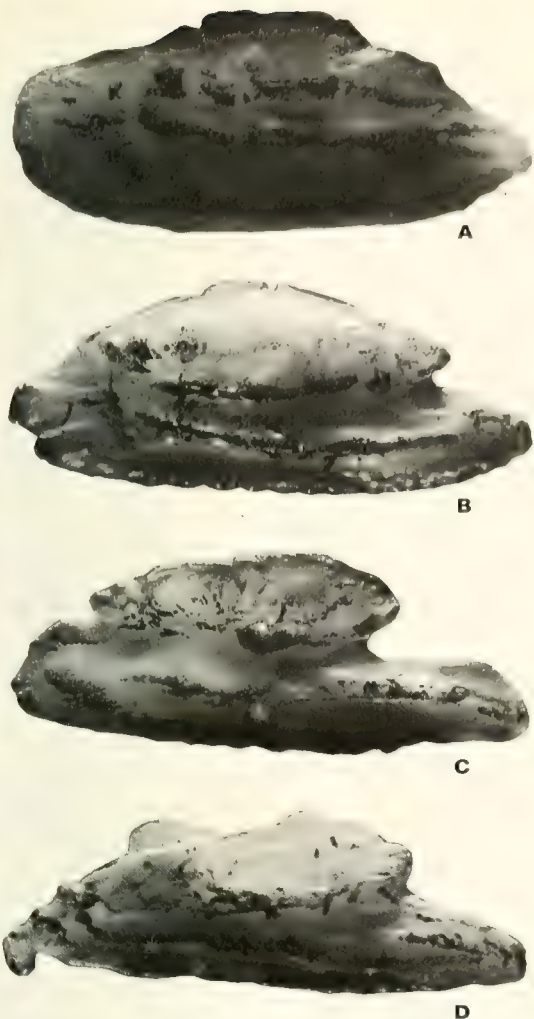


Figure 3. Left sagittae of four Californian trichiurids: a, *Aphanopus carbo* 7.5 mm; b, *Trichiurus nitens* 5.0 mm; c, *Lepidopus xantusi* 5.5 mm; d, *Assurger anzac* 3.0 mm. Photos by Jack W. Schott.

terial from oceanic areas of the Pacific, we are in no position to demonstrate "non-cline discontinuity," but the material we have examined does appear to add strength to the argument for retaining *T. nitens*. Nine specimens, from various localities between southern California and Panama, yielded the following fin ray and vertebral counts (corresponding counts for *T. lepturus* taken from Tucker [1956] are enclosed in parentheses): dorsal rays, 118–128 (126–137); anal rays, 95–97 (105–108); vertebrae, 148–155 (162–168). There are 36–38 dorsal fin rays to a vertical above the anus, and 34–36 of the vertebrae are precaudals.

Trichiurids frequently are fed upon by cetaceans, pinnipeds, tunas, bill-fishes, birds, and squid because conventional recognition characters rapidly disappear with digestion, otoliths often are the only identifiable fish remains to be found in the stomachs of these predators. The otoliths (sagittae) of the five Californian trichiurids (Fig. 3 and 3) illustrate close family relationships, especially in the configuration of the sulcus (i.e. groove on the inner face), yet they are also readily distinguishable from each other. The sagitta of *Aphanopus* lacks an antistrotrum (anterior projection above the sulcus) and is broadly rounded posteriorly. Sagittae of *Diplospinus* also lack an antistrotrum, but have a squared off notch at the posterodorsal corner. In *Trichiurus*, the greatest otolith height occurs near its midlength, and the outer face is deeply concave dorso-ventrally. In both *Lepidopus* and *Assurger*, the otolith is highest in front of the midpoint, but in *Assurger* the tapered posterior end turns abruptly downward. Even more spectacular is the relative length of the sagitta of these two genera: 3.0 mm in a 1534 mm SL *Assurger* and 5.5 mm in a 785 mm SL *Lepidopus*.

KEY TO CALIFORNIAN TRICHIURIDS

1. Caudal fin hair-like; ventral fins absent; lateral line well below mid-side on posterior three-fourths of body *Trichiurus nitens*
Caudal fin mackerel-like; ventral fins present, sometimes as spine-like scales or rudimentary and embedded; lateral line at mid-side on posterior three-fourths of body 2
2. Spinous and soft-rayed portions of dorsal fin completely separated, or separated by a distinct notch 3
Spinous and soft-rayed portions of dorsal fin continuous, indistinguishable without microscopic examination 4
3. Dorsal spines 30 to 34; dorsal soft-rays 35 to 40; vertebrae 59 to 61 *Diplospinus multispinatus*
Dorsal spines 42 to 43 (38 to 41 for Atlantic); dorsal soft-rays 54 to 55 (53 to 56 for Atlantic); vertebrae 105 *Aphanopus carbo*
4. Body 25 times as long as deep; dorsal rays 116 to 119; vertebrae 127 *Assurger anzac*
Body less than 15 times as long as deep; dorsal rays 78 to 81; vertebrae 84 to 87 *Lepidopus xantusi*

ACKNOWLEDGMENTS

Many individuals were helpful at one stage or another of our investigations concerning the family Trichiuridae. Over 30 different fishermen contributed directly by bringing in specimens that they caught, and although most of these are not acknowledged by name in the text we are deeply indebted to them. Others who were especially helpful were E. H. Ahlstrom, National Marine Fisheries Service, La Jolla; Charles R. Clothier (deceased); James E. Craddock, Woods Hole Oceanographic Institution; W. I. Follett, California Academy of Sciences; Shelly Johnson and Richard McGinnis, University of Southern California; Robert J. Lavenberg and Armando Solis, Natural History Museum of Los Angeles County; G. E. Maul, Municipal Museum, Funchal, Madeira; Richard Rosenblatt and Robert L. Wisner, Scripps Institution of Oceanography; and Jack W. Schott, California Department of Fish and Game. Research on otoliths has been supported by grants (GB-1244 and GB-6490) to Fitch from the National Science Foundation.

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ORGAN WEIGHTS OF NON-CAPTIVE PORPOISE (*STENELLA* SPP.)

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ABSTRACT: Weights of heart, lungs, liver, kidney, and spleen of 68 eastern Pacific spotted porpoise (*Stenella graffmani*) and 14 eastern Pacific spinner porpoise (*S. cf. S. longirostris*) are presented and related to total body weight. Values of Huxley's growth coefficient α are presented. Adult female spotted porpoise have on the average smaller spleens than adult males; a hypothesis of suppression of antibody production in pregnant females is suggested.

Information on organ weights and on other aspects of the anatomy of non-captive cetaceans is valuable for 3 reasons: 1) to establish norms that may be used in evaluation of the post-mortem condition of animals that die in captivity, 2) to further understanding of the physiology and overall biology of these animals, which is so radically different from that of terrestrial mammals, and 3) to provide comparative data for use in the systematics of the group.

Odontocete cetaceans for which various organ weights have previously been reported include *Phocoena phocoena*, *Tursiops truncatus*, *Lagenorhynchus acutus*, *Delphinus delphis*, *Grampus griseus*, *Delphinapterus leucas*, *Physeter catodon* (Slijper, 1959); *Globicephala melaena* (Cowan, 1966); and, very recently, *Inia geoffrensis* (Pilleri and Gihl, 1969b), and *Stenella styx* [= *S. coeruleoalba* (fide Mitchell, 1970)] (Gihl and Pilleri, 1969a). Layne (1965) reported weights of heart, lungs, liver, and kidneys for 1 specimen of *Stenella longirostris*. We report here weights of several organs for 68 eastern Pacific spotted porpoise, *Stenella graffmani* (Lönnerberg, 1934), and 14 eastern Pacific spinner porpoise, *Stenella cf. S. longirostris* (Gray, 1828). Specimens of the spotted *Stenella plagiodon* and *S. attenuata*, both very

similar to the eastern Pacific spotted porpoise, have been or are on exhibit or held captive for research purposes at various institutions on the southeast coast of North America and in Hawaii, respectively. Specimens of *Stenella roseiventris*, very similar to the eastern Pacific spinner porpoise, are currently held by aquaria in Hawaii.

METHODS

The specimens examined were all from the eastern tropical Pacific (Table 1). They were part of a large series of animals gathered for extensive studies of external morphometrics, osteology, parasites, and reproduction, which will be reported elsewhere. The porpoise were captured and killed accidentally during the course of commercial tuna seining operations, such as described by Perrin, 1969. The animals were placed in refrigerated holds along with the tuna and upon return to port were kept in freezers at -18° C until they could be dissected. Before dissection, the specimens

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TABLE 1. Collection data.

Date	Locality	Number of specimens		
		<i>Stenella graffmani</i>	<i>Stenella cf. S. longirostris</i>	Number of sexed
9 Apr. 1968	12°51' N/93°18' W	36	4	1
12 Apr. 1968	7°11' N/90°32' W	29	2	1
26-27 Mar. 1969	7°47'-8° N/106°36'-106°50' W	3	4	2
28 Apr. 1969	7°40'-8° N/107° W		2	2
5 Apr. 1969	8° N/109°45' W		2	1
Total		68	14	

TABLE 2. Total length, total weight, and organ weights of 68 specimens of *Stenella graffmani* and 14 specimens of *S. cf. S. longirostris*.

Specimen (field no.) / U. S. Nat. Mus. No. (skeleton)	Sex	Total length (cm)	Total weight (kg)	Heart (gm)	Lungs (gm)	Liver (gm)	Kidneys		Spleen (gm)
							Left (gm)	Right (gm)	
<i>Stenella graffmani</i>									
CV 259/395276	M	168	44.6	—	—	1000	(—409—)		43
CV 260/395277	F	175	58.2	—	—	1767	326	312	48
CV 261/395278	F	166	46.8	—	—	1283	182	205	44
CV 262/395279	F	165	43.2	—	—	1065	193	182	44
CV 263/395328	M	176	49.5	—	—	1259	235	251	51
CV 264/395329	M	172	50.0	—	—	1137	247	306	53
CV 265/395330	M	195	76.7	—	—	1727	326	353	54
CV 266/395331	M	168	47.2	—	—	1011	178	199	32
CV 267/395332	M	179	61.7	—	—	1398	246	234	39
CV 268/395333†	F	190	76.3	—	—	1480	250	240	46
CV 269/395334	F	184	59.9	—	—	1476	217	209	31
CV 270/395336†	F	182	70.8	—	—	1304	298	319	36
CV 271/395337	F	182	58.2	—	—	1467	245	251	35
CV 272/395338†	F	185	72.7	—	—	1394	242	—	16
CV 273/395339	M	163	47.2	—	—	1000	220	233	85
CV 274/395385	M	178	53.2	253	—	1153	232	208	24
CV 275/395386	M	157	42.2	230	—	1087	200	247	84
CV 276/395387	M	158	50.0	211	—	1274	216	201	45
CV 277/395388	F	182	59.9	291	—	1396	284	300	38
CV 278/395389	M	163	44.1	207	—	1237	190	199	62
CV 279/395390	M	218	84.0	311	—	1892	477	485	36
CV 280/395391	M	203	82.7	311	—	1961	406	429	46
CV 281/395392	F	174	43.2	214	—	1280	220	227	60
CV 282/395393	F	174	44.1	179	—	1052	207	199	32
CV 283/395394	M	202	79.9	308	—	2195	484	480	50
CV 284/395395†	F	193	71.3	250	—	1371	309	290	30
CV 286/395397	M	165	47.7	199	—	1112	190	233	100
CV 287/395417	M	173	53.6	261	—	1325	260	296	60
CV 289/395594	M	177	48.6	226	1576	1219	227	243	44
CV 290/395595	F	163	40.4	184	1270	924	166	183	27
CV 291/395596	F	193	63.6	293	—	1847	340	323	21
CV 292/395597	M	189	75.8	289	2275	1704	354	380	50
CV 293/395598	M	200	62.2	274	2129	1281	291	316	65
CV 295/395526	F	139	29.1	152	994	528	91	104	19
CV 296/395527	M	129	23.6	—	907	517	86	91	33
CV 297/395528	F	143	26.8	129	824	470	88	100	30
CV 298/395529	M	154	40.4	210	1323	1124	155	189	47
CV 300/395530	M	144	31.8	169	1019	647	114	121	38
CV 303/395532	M	143	29.5	141	1075	532	112	113	34
CV 304/395535	M	86	6.8	52	382	135	35	35	6
CV 305/395458	F	78	5.0	40	185	109	28	27	1
CV 306/395459	M	91	7.2	54	264	122	40	—	6
CV 307/395460	F	80	5.5	43	254	122	32	35	6
CV 308/395461	F	79	5.5	38	232	101	27	30	5
CV 309/395466	F	188	56.7	236	2078	1798	281	330	26
CV 310/395463	M	180	58.2	264	1642	1360	220	241	48
CV 311/395464	M	200	69.9	286	2090	1869	389	406	47
CV 312/395465	F	164	44.1	211	1317	1087	233	198	42
CV 313/395462	M	160	41.8	182	1291	999	177	179	62
CV 314/395467	F	184	55.4	284	1789	1600	284	290	20
CV 315/395468	M	162	43.6	227	1354	1139	193	190	35

TABLE 2. (Continued)

Specimen (field no.)/U. S. Nat. Mus. No. (skeleton)	Sex	Total length (cm)	Total weight (kg)	Heart (gm)	Lungs (gm)	Liver (gm)	Kidney		
							Left (gm)	Right (gm)	
CV 316/395603	M	168	45.0	211	1457	1013	187	209	60
CV 317/395604	M	138	25.9	147	887	614	121	117	34
CV 318/395605	F	144	29.6	160	1047	684	115	114	39
CV 319/395606	F	168	46.8	204	1681	974	200	222	72
CV 320/395607	M	167	46.3	210	1672	1132	205	217	76
CV 321/395608	M	153	34.6	175	1304	774	130	140	34
CV 322/395609	F	142	26.3	119	853	528	102	110	26
CV 323/395610	M	162	46.8	201	1700	1076	191	190	33
CV 324/395611	F	136	25.4	126	959	523	82	94	11
CV 325/395612	M	135	29.5	153	1090	608	94	108	43
CV 326/395613 ¹	M	86	6.6	42	246	104	33	31	3
CV 327/395614 ²	F	81	5.9	44	245	84	29	30	3
CV 328/395615 ³	M	74	3.4	29	156	62	21	28	2
CV 329/395616 ¹	F	81	5.7	—	—	—	26	26	4
PQ 01/395617	M	198	—	301	—	1234	231	247	42
PQ 02/395618	M	170	—	170	—	657	161	149	27
PQ 04/395410	F	168	—	219	—	995	197	176	27

Stenella cf. S. longirostris

CV 285/395369	F	177	44.5	230	—	936	150	158	15
CV 288/395593	F	173	43.5	220	—	832	(—300—)		23
CV 294/395526	F	149	33.6	204	1112	855	116	137	43
CV 299/395531	M	119	18.6	114	631	368	58	69	14
CV 301/395533	F	140	26.3	135	812	542	73	88	16
CV 302/395534	M	118	18.1	97	599	367	60	63	29
PQ 03/395409	F	157	39.5	225	—	832	128	128	22
PQ 05/395411	F	168	46.7	196	—	971	147	164	13
PQ 06/395412 [†]	F	173	51.3	245	—	776	125	136	21
PQ 07/395413	F	176	52.2	191	—	871	145	144	—
PQ 08/395414	M	173	50.3	240	—	972	152	147	20
PQ 09/395599	M	173	59.0	272	—	997	192	201	31
PQ 10/395600	F	109	18.1	97	—	323	55	58	22
PQ 11/395601	F	105	13.2	72	—	282	46	51	10

[†] Individual was pregnant.¹ Fetus from CV 270/395336.² Fetus from CV 268/395333.³ Fetus from CV 272/395338.¹ Fetus from CV 284/395395.

were weighed on platform scales, accurate to the nearest pound. The weights were converted to kilogram equivalents for use here. Some dehydration may have taken place during the storage periods, which ranged from 5 days to 14 months. When each specimen was dissected, the heart, lungs, liver, kidneys, and spleen were excised, placed in plastic bags, and refrozen. The sample size is not the same for all the organs, as these data were gathered incidentally to the primary purposes of the dissections, and some organs were not removed when time was short for other procedures. Later, the organs were thawed and weighed on a beam balance, accurate to the nearest

gram. Four of the female specimens of *S. graffmani* collected on April 9, 1958 were gravid with near-term fetuses, and the organs of these fetuses were included in the sample. Degree of sexual development was determined by histological examination of gonads. Complete skeletons of all the specimens are in the U. S. National Museum, Washington, D. C., and museum numbers are given in table 2.

The taxonomy of the spotted and spinner porpoises is confused (Perrin and Hunter, 1972), and the use here of *Stenella graffmani* and *S. longirostris* is provisional pending the results of studies underway by Perrin and others.

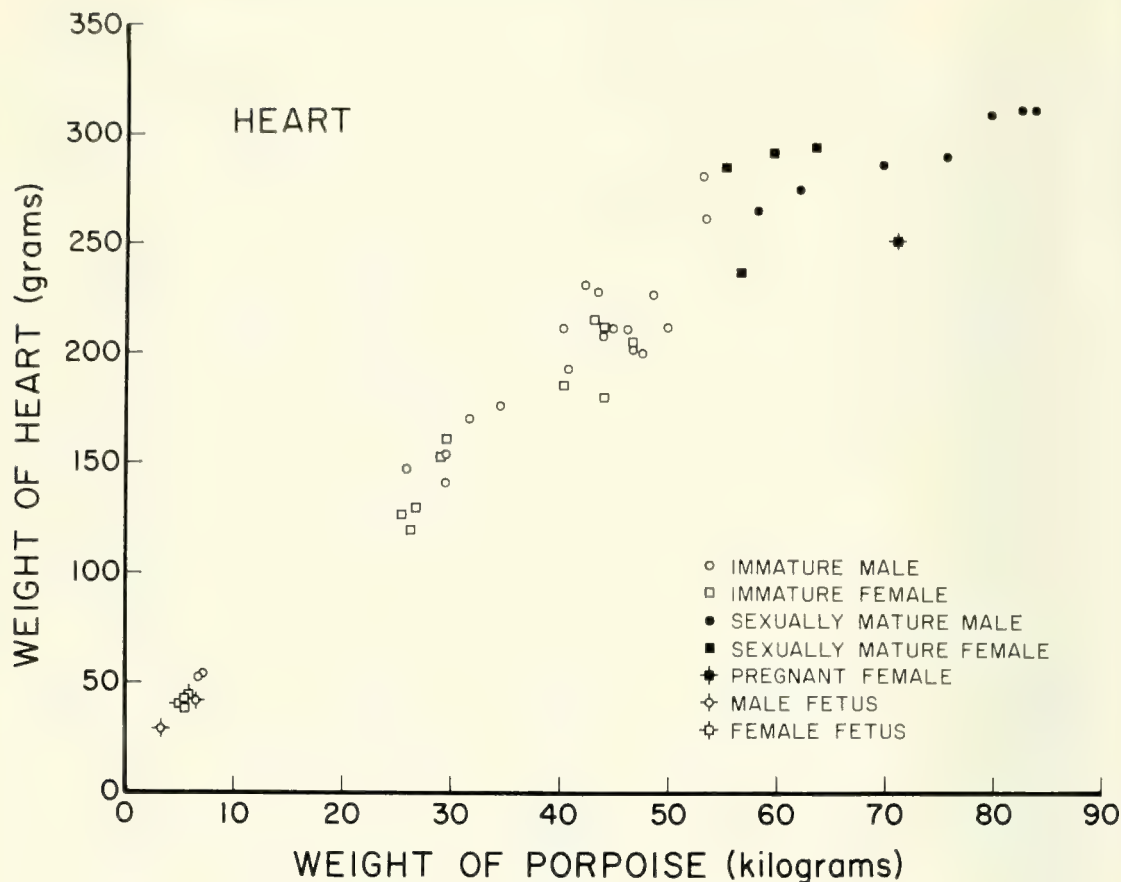


Figure 1. *Stenella graffmani*. Weight of heart relative to total body weight for 29 males and 19 females.

RESULTS

The data are presented in table 2. Scatter plots of organ weight on total weight are presented in figures 1-6 and 8-10. Where sample sizes were adequately large, the data were fitted to the equation $\text{Log } Y = a + b \text{ Log } X$ by the least squares method, where Y = organ weight in grams, X = total weight in grams, and b = Huxley's (1932) "growth coefficient" α . For the cases where correlation was statistically significant (at $P = 0.05$), the estimates of a and b are presented in table 3. Data for the pregnant females were not included in the regression analyses.

Heart

S. graffmani (Fig. 1). The hearts of 11 sexually mature adults (ranging from 180-218 cm total length and from 55.5-84.0 kg) weighed from 236-311 gm and from 0.37-0.51% (average: 0.43%) of total body weight. As is evident in figure 1, the relative weight of the heart decreases during development; the average relative weight for 28 calves and sexually immature subadults (ranging from 126-178 cm total length and from 25.4-53.6 kg total weight) was 0.48% (range: 0.41-0.57%) and for 8 infants and fetuses was 0.75% (range: 0.63-0.86%).

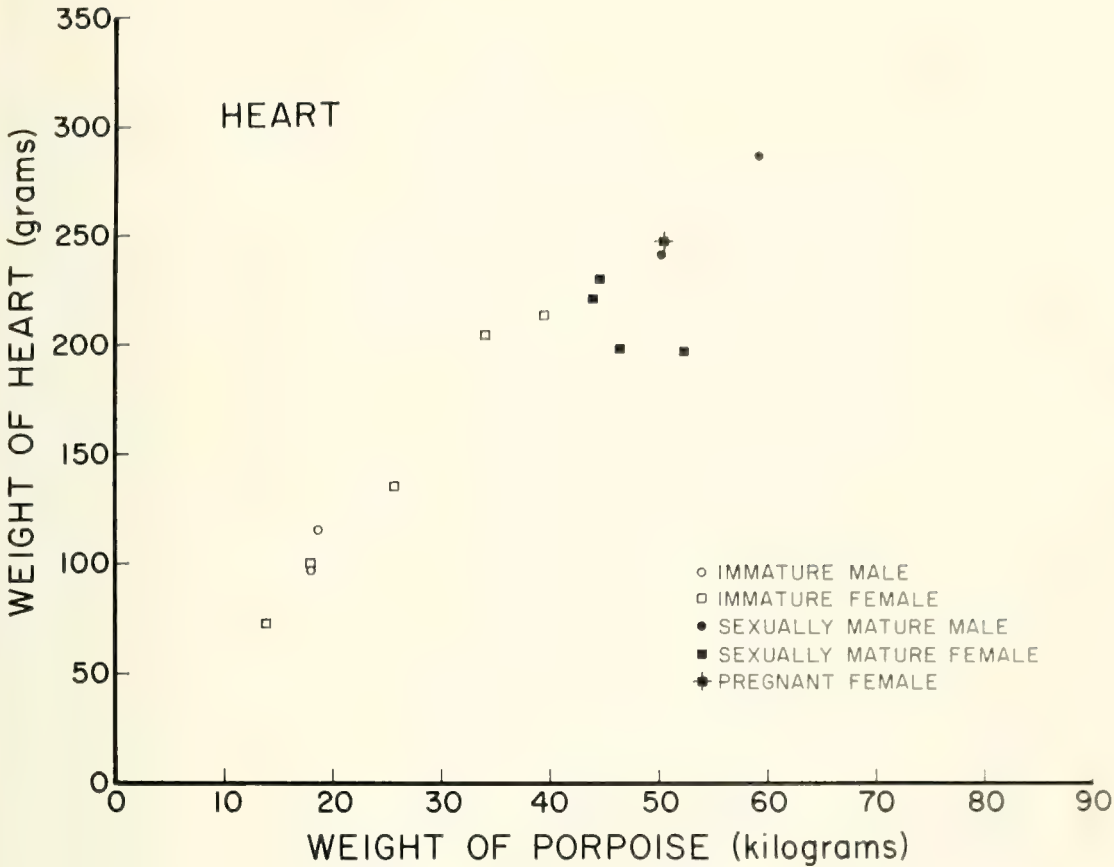


Figure 2. *Stenella* cf. *S. longirostris*. Weight of heart relative to total body weight for 4 males and 10 females.

TABLE 3. Log-log regression analyses of relationships between organ weights and total body weight in *S. graffmani* and *S. cf. S. longirostris*.

	a ¹	b ¹	r ¹	Sample size
<i>S. graffmani</i>				
Heart	-1.25	0.769	0.948	47
Lungs	-0.92	0.880	0.990	35
Liver	-2.18	1.114	0.922	59
Kidneys	-1.87	0.965	0.977	57
Spleen:				
males	-3.07	1.010	0.874	36
females	-3.40	1.057	0.885	24
<i>S. cf. S. longirostris</i>				
Heart	-1.48	0.820	0.962	13
Lungs	-1.25	0.947	0.991	4
Liver	0.01	0.608	0.536	13
Kidneys	-1.91	0.940	0.986	13

¹ Values of a, b, and correlation coefficient r in linear regression equation Log Y = a + b Log X, where Y = organ weight and X = total body weight, in gms.

S. longirostris (Fig. 2). The hearts of 6 sexually mature adults (ranging from 168–177 cm total length and from 43.5–59.0 kg total weight) weighed from 191–272 gm and from 0.37–0.52% (average: 0.46%) of total body weight. The data are insufficient to determine whether relative weight of the heart decreases during development in this species.

Lungs

S. graffmani (Fig. 3). The combined weight of both lungs of 6 adults (from 180–200 cm total length and from 55.4–75.8 kg total weight) ranged from 1642–2275 gm and from 2.82–3.66% (average: 3.19%) of total weight.

S. longirostris (Fig. 3). The lungs of 4 individuals, all calves and subadults (from 118–149 cm total length and from 18.1–33.6 kg total weight) weighed from 599–1112 gm and from 3.09–3.39% (average: 3.28%) of total weight.

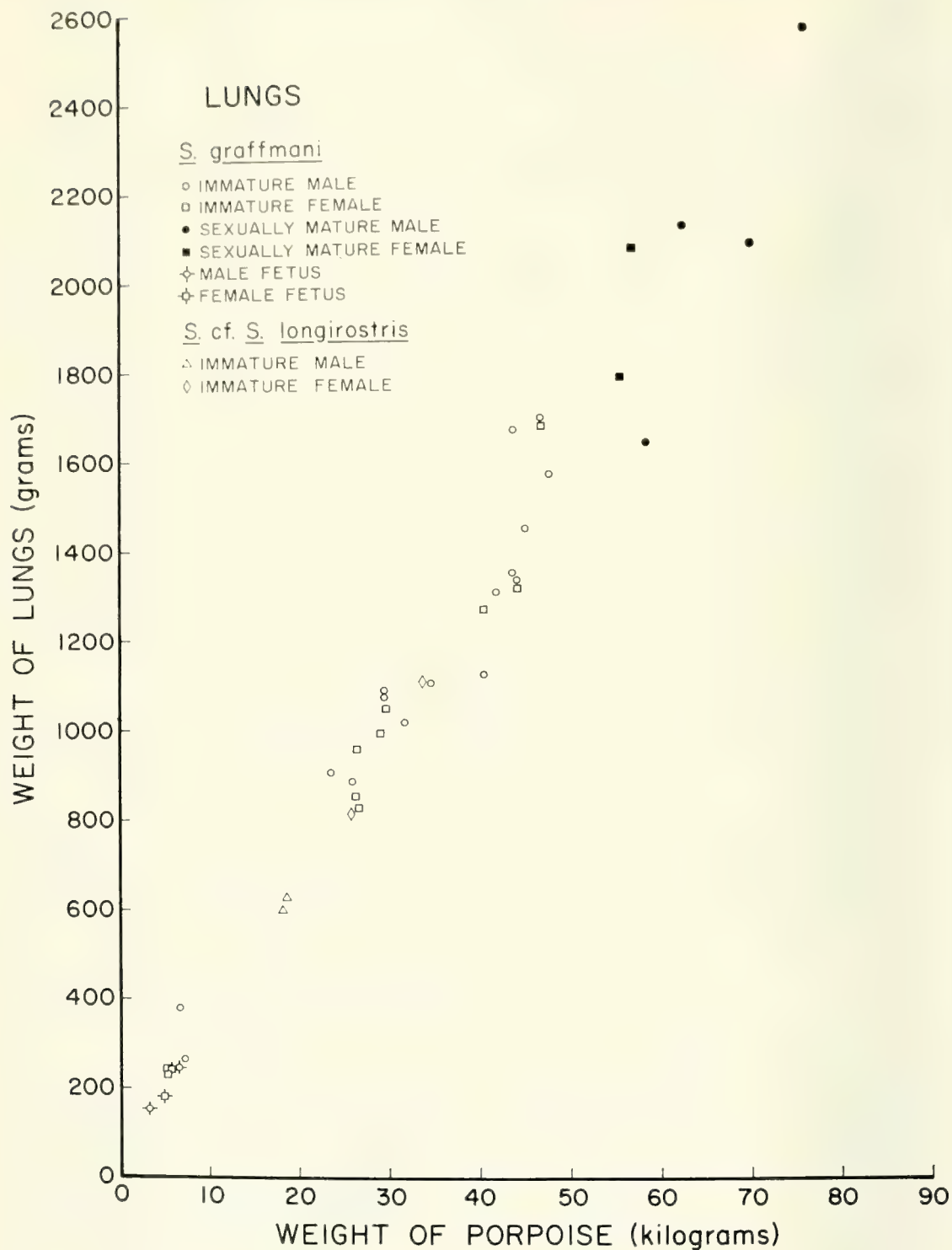


Figure 3. *Stenella graffmani*. Weight of lungs relative to total body weight for 22 males and 15 females. *Stenella cf. S. longirostris*. Weight of lungs relative to total body weight for 2 males and 2 females.

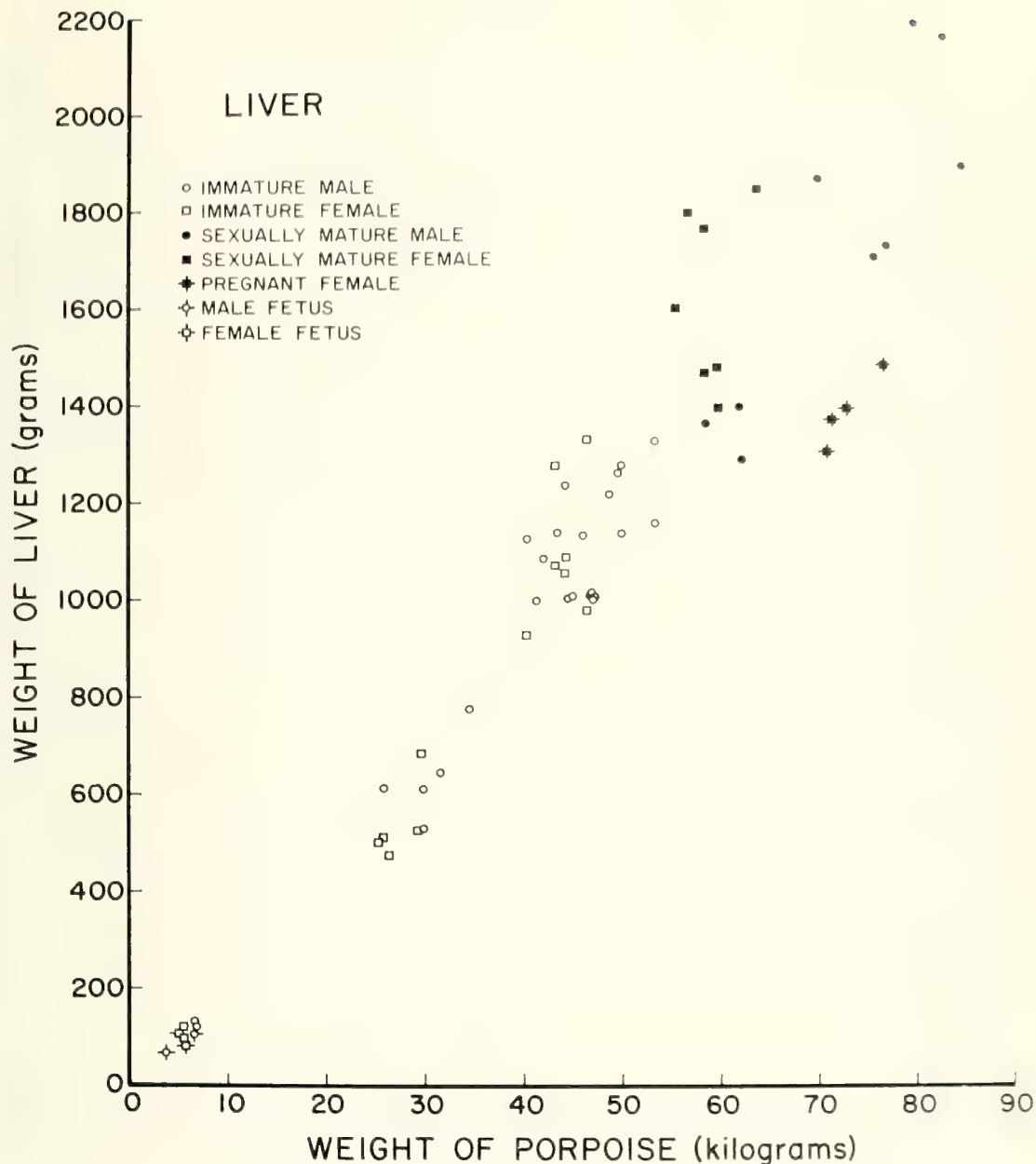


Figure 4. *Stenella graffmani*. Weight of liver in 36 males and 27 females.

Liver

S. graffmani (Fig. 4). The livers of 16 adults (from 175–218 cm total length and from 55.4–84.0 kg total weight) weighed from 1281–2195 gm and from 2.06–3.17% (average: 2.53%) of total weight. Relative weight of the liver appears

to increase early in development (average for 8 fetuses and infants was 1.84%, range 1.42–2.22%) and remain nearly constant thereafter.

S. longirostris (Fig. 5). The livers of 8 adults (168–177 cm total length and 43.5–59.0 kg total weight) weighed from 832–997 gm and from 1.87–2.10% (average: 1.90%) of total weight. Adults

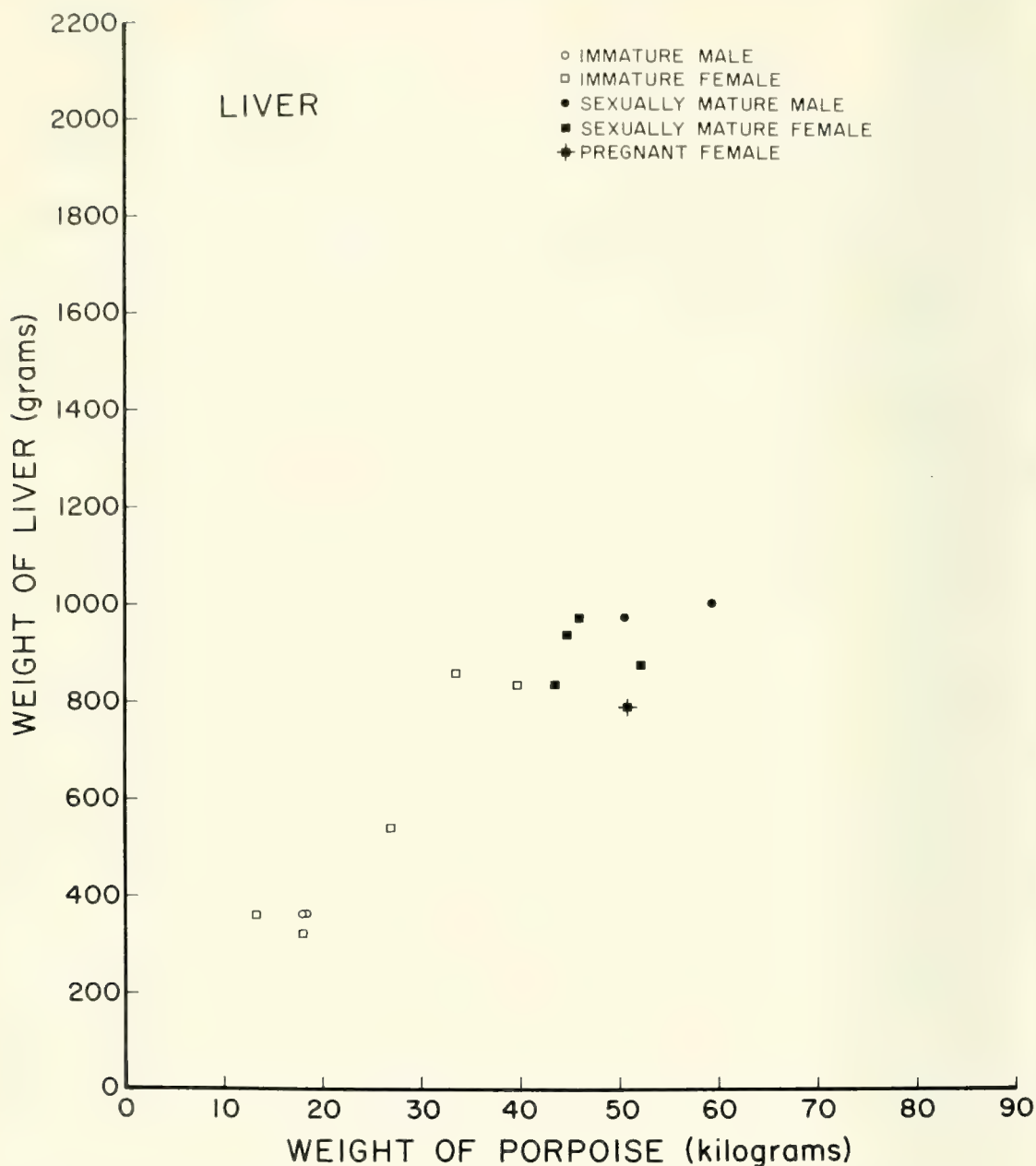


Figure 5. *Stenella* cf. *S. longirostris*. Weight of liver relative to total body weight for 4 males and 10 females.

of this species have smaller livers than subadults of *S. graffmani*; the livers of 21 calves and subadults of *S. graffmani* ranging from 43.2–53.6 kg total weight weighed from 974–1457 gm and from 2.08–3.00% (average: 2.42%) of total weight.

Kidneys

S. graffmani (Fig. 6). The relative weight of the kidneys drops from a high at birth to a low in calves and subadults and then increases again to a secondary high in adults. The kidneys of 8

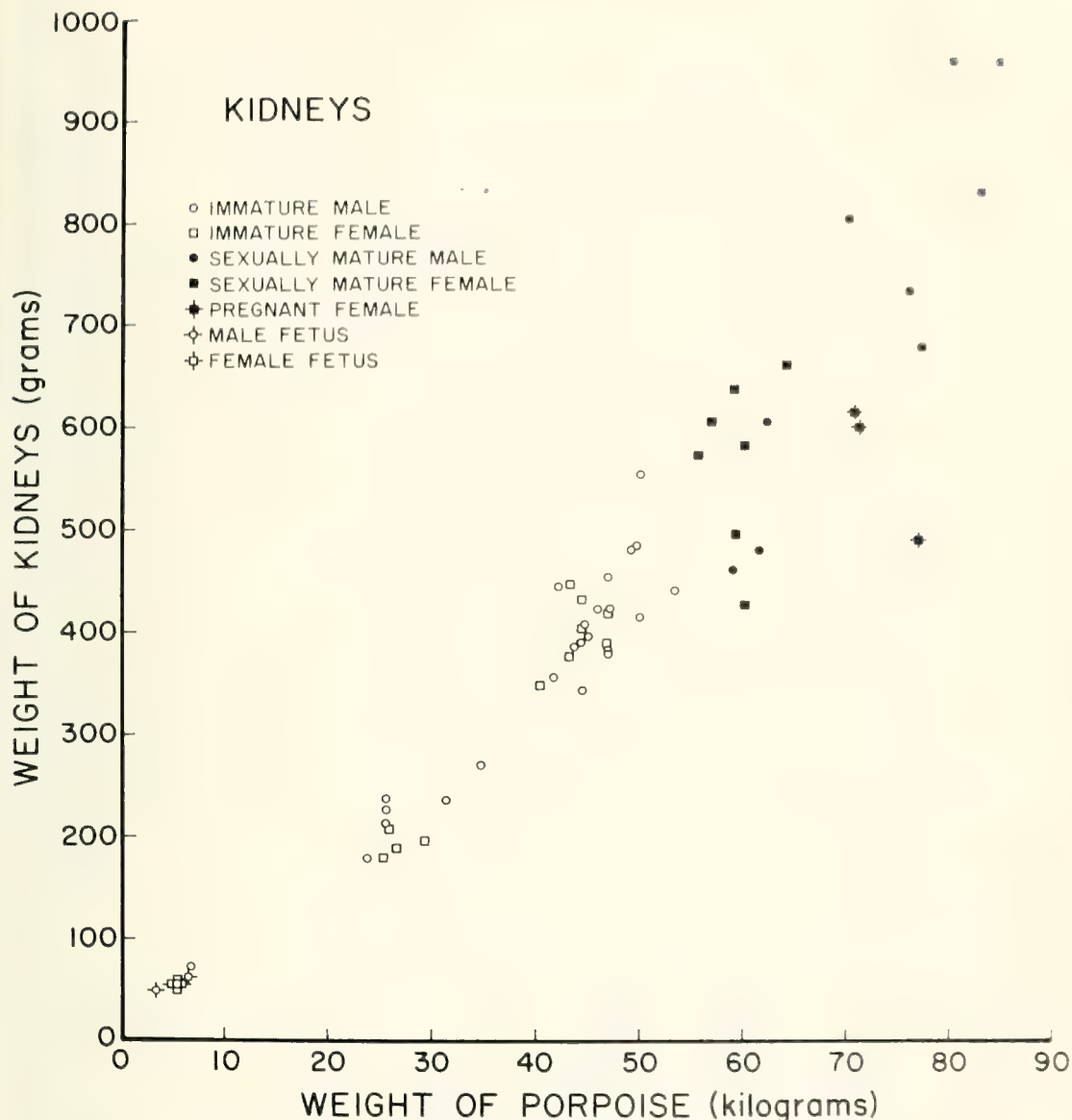


Figure 6. *Stenella graffmani*. Combined weight of kidneys relative to total body weight for 35 males and 27 females.

neonatal and near-term fetuses (74–86 cm total length and 3.4–6.8 kg total weight) ranged from 49–70 gm (average: 59 gm) and from 0.91–1.44% (average: 1.09%) of total weight. The kidneys of 31 calves and subadults (129–178 cm total length and 23.6–53.2 kg total weight) ranged

from 129–178 gm and from 0.67–1.11% (average: 0.84%) of total weight, and those of 15 adults (175–218 cm total length and 55.4–84.0 kg total weight) ranged from 426–968 gm and from 0.78–1.20% (average: 0.98%) of total weight. The animal is asymmetrical with respect to weight of

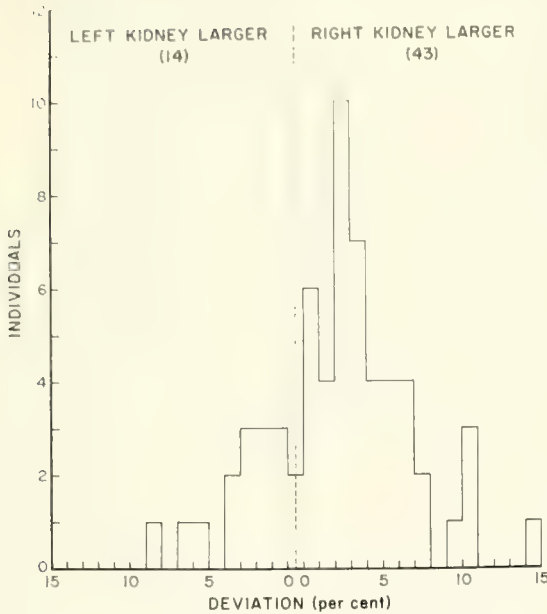


Figure 7. *Stenella graffmani*. Frequency distribution of percent deviation of weight of largest kidney from average weight of both kidneys, for 59 individuals.

kidneys (Fig. 7); the right kidney on the average is 2–4% heavier than would be expected were symmetry to prevail.

S. longirostris (Fig. 8). The kidneys of 6 adults (168–177 cm total length and 43.5–59.0 kg total weight) weighed from 289–393 gm and from 0.55–0.69% (average: 0.65%) of total weight. This species also exhibits dextral asymmetry; of 12 sets of kidneys weighed, in 9 the right kidney was heavier, in 2 the left was heavier, and in 1 set both kidneys weighed the same.

Spleen

S. graffmani (Fig. 9). We infer from the scatter plot of weight of spleen on total weight that the spleen increases in size both absolutely and relatively during development to a peak in subadulthood, then rapidly decreases in size, again both absolutely and relatively, to a relative low during adulthood. The spleens of 10 neonatals and near-term fetuses averaged 4 gm (0.07%) in weight, those of 11 calves (129–153 cm total length and 23.6–34.6 kg total weight) ranged from 11–43 gm (average: 31 gm) and from 0.04–0.15% (average: 0.11%) of total weight,

and those of 25 subadults (154–178 cm total length and 40.4–53.6 kg total weight) ranged from 24–100 gm (average: 53 gm) and from 0.05–0.21% (average: 0.12%) of total weight—the variance was greatest for this group, but the spleens of 16 adults (175–218 cm total length and 55.4–84.0 kg total weight) weighed only 20–65 gm (average: 41 gm) and from 0.03–0.10% (average: 0.06%) of total weight. There is also an apparent sexual dimorphism in weight of the spleen in adults; the spleens of 9 adult males weighed 36–65 gm (average: 48 gm) and 0.04–0.10% (average: 0.06%) of total weight, while those of 7 non-pregnant adult females weighed only 20–48 gm (average: 31 gm, the same as for the calves) and from 0.03–0.08% (average: 0.05%, less than for the infants and fetuses). The smallest adult spleen (16 gm or 0.02% of total weight) was possessed by a pregnant female (near-term).

S. longirostris (Fig. 10). As is the case for the liver and the kidneys, the adults of this species possess smaller spleens than do subadults of comparable size of *S. graffmani*. The spleens of 5 adults weighed 13–31 gm (average: 30 gm) and from 0.03–0.05% (average: 0.04%) of total weight. The data conform to the pattern noted above for *S. graffmani* of decreased absolute weight of spleen in adulthood but are insufficient in number to warrant conclusions.

DISCUSSION

The value of the growth coefficient *b*, the ratio of the rate of increase of organ weight to the rate of increase of total body weight, for heart weight obtained here for *S. graffmani* (0.769) is lower than those obtained by Pilleri (1969) for *S. coeruleoalba* (1.014), *Delphinus delphis* (0.806), and *Phocoena phocoena* (1.055). That of *S. longirostris* (0.820) falls between those for *D. delphis* and *S. coeruleoalba*. The value of the growth coefficient for lung weight appears to be inversely related to maximum body weight. Of the 3 species of *Stenella*, the smallest, *S. longirostris*, has the highest coefficient (0.947), and the largest, *S. coeruleoalba* has the lowest (0.684)—Pilleri, 1969. The value of *b* for *S. graffmani* is intermediate (0.880). The value of *b* for liver weight for *S. longirostris* (0.608) is close to that obtained for *S. coeruleoalba* (0.684) by Pilleri, but that for *S. graffmani* (1.114) is considerably

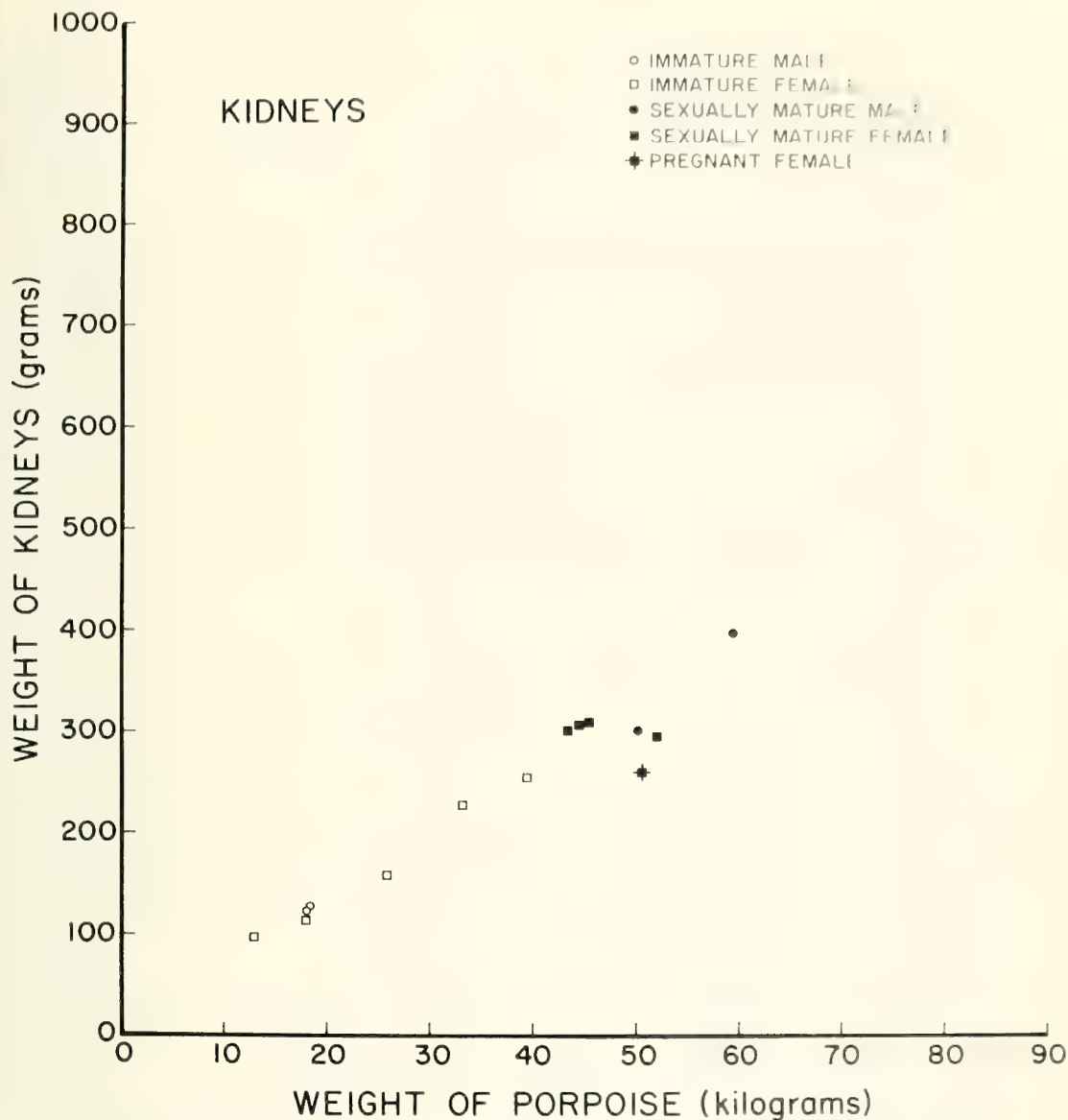


Figure 8. *Stenella* cf. *S. longirostris*. Weight of kidneys relative to total body weight for 4 males and 9 females.

higher. The values of b for kidney weight for both species dealt with here (0.965 and 0.940) are lower than those obtained by Pilleri for *S. coeruleoalba* (0.977) and *D. delphis* (1.089).

Pilleri's (1969) value of b for *Phocoena phocoena* (0.685) is very much lower than those for the 4 delphinids (*sensu stricto*).

The odontocete spleen has a relatively large

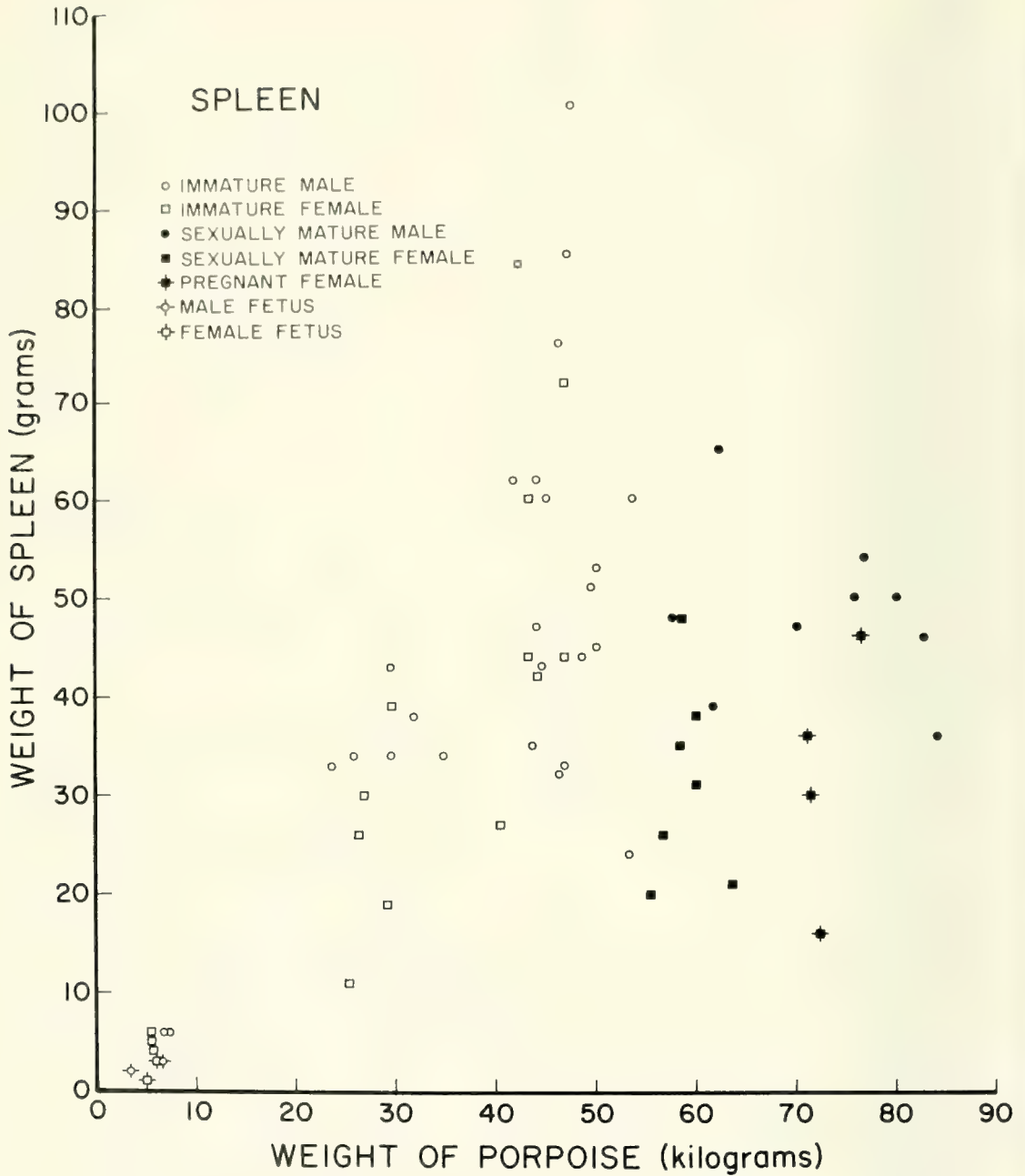


Figure 9. *Stenella graffmani*. Weight of spleen relative to total weight for 37 males and 28 females.

number of lymph nodules (white spleen pulp) (Pilleri, 1969). A major function of the lymphatic tissue of the spleen is the production of antibodies (Jubb and Kennedy, 1963). We offer here the tentative hypothesis that smaller relative spleen size for adult females of *S. graffmani* (Fig. 8) is

tied functionally to suppression of antibody production during pregnancy to eliminate the possibility of rejection of the fetus. Obviously histological investigation of splenic change during pregnancy will be necessary if this hypothesis is to be critically examined.

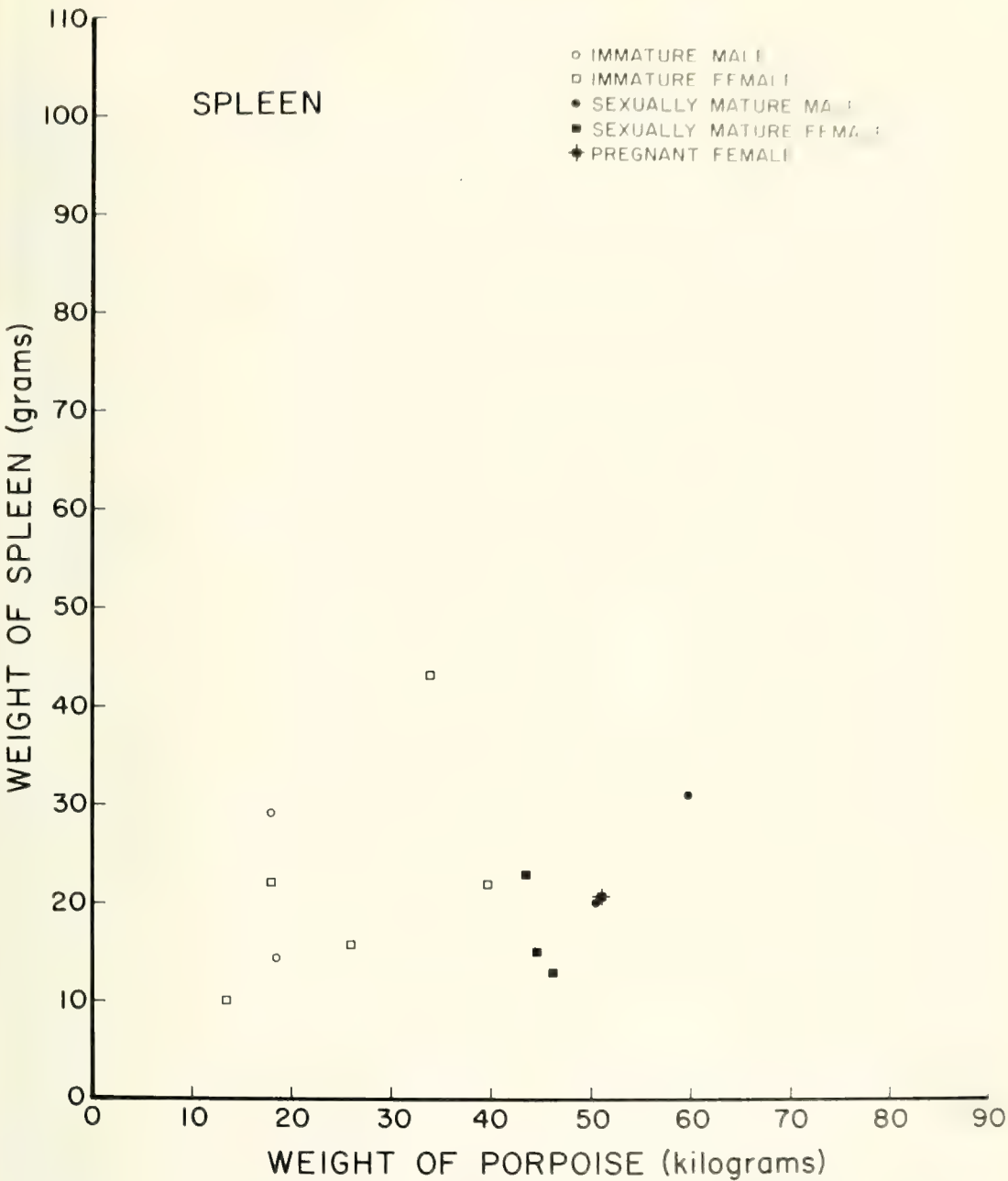


Figure 10. *Stenella* cf. *S. longirostris*. Weight of spleen relative to total weight for 4 males and 9 females.

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THE EFFECTS OF LOWERED DISSOLVED OXYGEN CONCENTRATIONS AND SALINITY ON THE FREE AMINO ACID POOL OF THE POLYCHAETOUS ANNELID *NEANTHES ARENACEODENTATA*

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ABSTRACT: An inbred strain of the polychaetous annelid *Neanthes arenaceodentata* was subjected to reduced dissolved oxygen and salinity levels under laboratory conditions and effects of these treatments on the free amino acid pool studied. Changes in the relative proportions of free amino acids were observed after exposure to lowered dissolved oxygen concentrations. It is hypothesized that these relate to changes in total protein levels and conversion to energy production under anaerobic conditions. The total free amino acid concentration, expressed as total optical density of ninhydrin positive spots, decreased at lowered salinities along with alteration in the relative proportions of amino acids. These changes probably relate to osmoregulation by the worm under reduced salinities.

The free amino acid pool is a major constituent of the metabolic machinery of an organism, and therefore gives a good measure of metabolic activity. It is also unique to each species and has been compared to a human fingerprint (Roberts and Lowe, 1954). The free amino acid pool has been used as a research tool in the study of diseases (Roberts and Frankel, 1949; Roberts and Borges, 1955), in the study of speciation (Ball and Clark, 1953; Micks, 1954, 1956; Micks and Gibson, 1957; and Lewallen, 1957), and in measuring environmental effects on organisms (Schafer, 1961, 1963; Lynch and Wood, 1966; Stephens and Virkar, 1966; and Clark, 1968a).

In his review of the free amino acid pool in invertebrates, Awapara (1962), noted that high

concentrations were measured in marine mollusks and crustaceans and correspondingly low concentrations in terrestrial and fresh water species of these groups. He concluded that free amino acids and taurine formed the bulk of the alpha amino nitrogen found in the body fluids of most marine invertebrates. Clark (1968b) substantiated these findings in her study of 14 species of polychaetes. She also noted that a great variability occurred between related species. Therefore, the free amino acid pool in marine invertebrates can be characterized: 1) the pool is large and differs from one species to another, 2) the pool has high con-

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centrations of a few forms (glycine and proline, for example) and low concentrations of a large number of amino acids, and 3) the pool is significantly small in terrestrial and fresh water species. Awapara (1962) postulated that the free amino acid pool of marine invertebrates may function both as an osmoregulatory device and as a possible food reservoir. The work of Stephens and Virkar (1966) may be cited as evidence for the role of the pool as an osmoregulatory device. They found that a decline in salinity lowered the total concentration of the free amino acids, the uptake of free amino acids from the surrounding medium was decreased under lowered salinities, and an increase occurred in the rate of assimilation of amino acids into proteins under lowered conditions. The second postulate of Awapara can be supported by the uptake of free amino acids from an ambient medium and their possible role as a nutrient source (Stephens, 1963; Stephens and Virkar, 1966; Reish and Stephens, 1969).

Investigations of the effects of environmental stress on the free amino acid pool include studies on varying salinities (Lynch and Wood, 1966; Stephens and Virkar, 1966; Negus, 1967; Clark, 1968a) and domestic sewage (Schafer, 1961, 1963). As discussed above, decreased salinities cause a decrease in the total free amino acid pool to a specific level (Lynch and Wood, 1966); conversely, in hypersalinities, the concentration of the pool increases with proline, glycine, and alanine accounting for most of the increase. Furthermore, Negus (1967) found that the oxygen consumption increased under decreased salinities in the pelecypod *Hydrobia ulvae* presumably as a response to an increase in energy requirements. Allen (1961) suggested that an increase in energy expenditure would supply short-chain keto acids which could be used as substrates in the transaminase reaction. The amino acids from hydrolyzed protein would serve as amino donors. In addition, Clark (1968b) pointed out that amino acids may be transferred into tissue compartments depending upon the ambient salinity which would then act as a osmoregulatory mechanism.

Environmental stresses affect the organism at sublethal levels. Boring activity in the marine wood borer genus *Limnoria* was found to be related to the salinity; boring activity decreased with a decrease or increase in salinity (Eltringham, 1961; Reish and Hetherington, 1969). Similar results were obtained when three species of *Limnoria* were subjected to sublethal levels of reduced dissolved oxygen concentrations (Anderson and

Reish, 1967). Egg production was suppressed by hemoglobin compensation occurred in *Neanthes arenaceodentata* when it was subjected to lethal concentrations of dissolved oxygen (Dunham, 1969; Raps and Reish, 1971).

The laboratory induced changes in the organism discussed above serve to indicate that metabolic changes may be occurring within the organism and that perhaps changes at the organismic level and molecular level can be correlated. Therefore, it is the purpose of this study to measure the effects of lowered dissolved oxygen concentrations and lowered salinities on the free amino acid pool of an inbred strain of *Neanthes arenaceodentata* and to correlate these results with those previously gathered with this species on the organismic level. Furthermore, it is hoped that we can learn more about the basic effects of environmental stress on an organism which may then be employed as a monitoring measure of marine pollution.

METHODS

The Reish strain of *Neanthes arenaceodentata* (Moore) was chosen as the experimental animal because of its uniform genetic background. The stock colony was fed powdered alfalfa and the green alga *Enteromorpha crinita* during the experiments.

The procedure was essentially the same for both the dissolved oxygen and salinity experiments with only minor differences. For each experiment four young males and four females were selected by use of the fighting response (Reish and Alosi, 1957). Each worm was placed into a separate 250 ml erlenmeyer flask with 100 ml filtered sea water and sufficient food (dried, resoaked *Enteromorpha crinita*). The flasks were sealed with a rubber stopper and in the case of the dissolved oxygen experiments each flask was flushed with N₂ gas according to the method of Reish and Richards (1966). Reduced chlorinity conditions were made by diluting 100% sea water (19.2 ‰ chlorinity) to 90% (16.4 ‰) and 70% (12.8 ‰). All flasks were kept in a cold bath at 18° C for seven days. At seven days, in the case with the dissolved oxygen experiments, the rubber stopper was removed and the dissolved oxygen measured with an electrode. The worms were removed from the flasks and placed into separate vials containing 80% ethanol.

Extraction of amino acids was accomplished by leaving the worms in the 80% ethanol for 48 to 50 hours. The worms were removed from the

TABLE 1. Means, standard deviations,¹ and Student *t*-test² of the 14 most abundant amino nitrogen compounds at varying concentrations of dissolved oxygen.

Amino Acid Spot	Control (5.8 mg/l) Means, S.D.	2.7 mg/l Means, S.D.	<i>t</i> -test	1.46 mg/l Means, S.D.	<i>t</i> -test	0.83 mg/l Means, S.D.	<i>t</i> -test
Aspartic Acid	2.40 ± 1.27	2.08 ± 0.61	1.25	2.13 ± 0.52	1.19	0.70 ± 0.33	4.47**
Glutamic Acid	2.77 ± 0.96	2.73 ± 0.74	0.11	3.72 ± 0.64	2.87**	2.87 ± 0.72	0.29
L-amino Adipic Acid	0.47 ± 0.30	0.23 ± 0.20	0.00	0.52 ± 0.20	0.00	0.28 ± 0.31	0.00
Serine	4.04 ± 1.11	3.81 ± 0.87	0.54	3.46 ± 0.95	1.34	2.67 ± 0.66	3.60**
Glycine	29.03 ± 6.00	37.64 ± 8.65	2.71*	32.14 ± 8.83	0.96	22.65 ± 7.61	2.18*
L-threonine	3.51 ± 1.19	1.12 ± 0.63	6.28**	1.77 ± 1.26	3.48**	3.96 ± 1.65	0.75
Glutamine	2.65 ± 0.96	3.17 ± 1.17	1.18	2.84 ± 1.04	0.46	2.26 ± 0.59	0.25
Citrulline	0.55 ± 0.22	2.00 ± 1.20	4.02**	0.92 ± 0.83	1.54	0.83 ± 0.46	2.00
L-alanine	2.92 ± 0.96	2.05 ± 1.06	2.07*	2.14 ± 1.59	1.41	5.30 ± 2.17	3.35**
Tyrosine	3.14 ± 0.89	1.37 ± 1.07	4.31**	2.99 ± 1.40	0.30	2.38 ± 0.80	2.23*
Valine, norvaline, L-methionine	5.35 ± 2.61	3.21 ± 1.97	2.18*	4.42 ± 2.51	0.85	6.42 ± 3.23	0.85
Phenylalanine, leucine, isoleucine	11.04 ± 4.29	7.63 ± 5.26	1.67	6.97 ± 4.68	2.08*	12.79 ± 6.85	0.72
Asparagine	3.12 ± 0.93	2.87 ± 1.15	0.58	3.21 ± 0.90	0.24	2.08 ± 0.95	2.73*
Proline	14.35 ± 4.65	16.64 ± 3.84	1.26	15.99 ± 3.05	0.98	24.45 ± 4.66	5.10*

¹ Means and standard deviations recorded as per cent values² Compared to control

* 5% level: 2.07

** 1% level: 2.82

ethanol, weighed, and inspected for possible damage. Specimens with openings in their body wall were discarded.

Chromatographic Techniques: The chromatographic techniques employed followed essentially the procedure given by Mearns and Reish (1969). Dowex 50W, X8, 100–200 mesh ion exchange resin was prepared in 4 N NaOH 12 hours prior to use. This resin was washed to neutral with glass distilled water and activated 30 minutes prior to use with 4 N HCl. Each of the eight 200 × 15 mm polyethylene drying columns was filled with 6 ml of resin and the flow rate adjusted with glass wool. The column was washed with 25 ml glass distilled water and 2.5 ml extract was pipetted into a tube. The salts were eluted with 125 ml of glass distilled water in 25 ml aliquots and discarded. Then 12.5 ml of 4 N NaOH was pipetted into each column to elute the amino acids into collecting tubes. The contents of each tube was condensed to 0.05 ml by use of a rotary evaporation. The spotting procedure, the chromatography, and development of the chromatograms were identical to Mearns and Reish (1969).

The ninhydrin-positive spots were identified from a previously prepared chromatographic master. After identification, the spots were cut out and placed into individual vials containing 10 ml 50% ethanol for 2 hours. The paper was then removed and each eluate was analyzed quantitatively with a spectrophotometer. Optical densities

were read at 570 m μ wavelength for the purple and pink spots and at 300 m μ for the orange and yellow spots and adjusted for the 50% ethanol blank. The optical densities were recorded and converted to relative proportions of the total optical density according to the procedure given by Hrubant (1959). The relative proportions of amino acids or ninhydrin-positive spots from each chromatogram were compared using the Student *t*-test.

RESULTS

The data are summarized in tables 1 and 2 for the dissolved oxygen and salinity experiments, respectively, as the means, standard deviations, and Student *t*-tests. The optical densities for each amino acid are not included in the tables; they have been converted to per cents of total optical density. Since nine of the 23 amino acids for the dissolved oxygen experiments and ten of the 23 for the salinity experiments were discernible but negligible these data were omitted from the tables.

Dissolved oxygen experiments: At least 12 and, since some spots contained more than one amino acid, possibly 16 amino nitrogen compounds were significantly different from the controls to at least the 5% level on the Student *t*-test scale after lowered concentrations of dissolved oxygen over a seven day period. At the mean D.O. level of 2.71 mg/l, six and possibly eight compounds

TABLE 2. Means, standard deviations¹ and Student *t*-test² of the 13 most abundant amino nitrogen compounds under varying salinities.

Amino Acid Spot	Control (normal salinity) Means, S.D.	90% Salinity Means, S.D.	<i>t</i> -test	70% Salinity Means, S.D.	<i>t</i> -test
Aspartic Acid	2.40 ± 1.27	1.62 ± 1.50	1.34	1.60 ± 0.82	1.76
Glutamic Acid	2.77 ± 0.96	2.21 ± 0.57	1.69	1.60 ± 0.69	0.29
Serine	4.04 ± 1.11	4.27 ± 1.25	0.46	3.79 ± 0.57	0.6
Glycine	29.03 ± 6.00	42.18 ± 7.92	4.39**	43.58 ± 10.73	3.86**
L-threonine	3.51 ± 1.19	1.74 ± 1.12	3.76**	3.16 ± 2.13	0.48
Glutamine	2.65 ± 0.96	1.75 ± 0.57	2.72*	1.27 ± 0.75	3.83**
Citrulline	0.55 ± 0.22	0.80 ± 0.46	1.78	0.85 ± 0.92	1.15
L-alanine	2.92 ± 0.96	2.49 ± 1.40	0.86	1.58 ± 1.27	2.91**
Tyrosine	3.14 ± 0.89	1.74 ± 1.30	3.04**	1.54 ± 1.14	3.80**
Valine, norvaline, L-methionine	5.35 ± 2.61	2.81 ± 1.41	2.85**	3.96 ± 2.49	1.28
Phenylalanine, leucine, isoleucine	11.04 ± 4.29	6.25 ± 3.36	2.92**	7.57 ± 5.53	1.64
Asparagine	3.12 ± 0.93	3.62 ± 0.84	1.38	3.25 ± 0.84	0.36
Proline	14.35 ± 4.65	16.61 ± 3.58	1.28	13.38 ± 3.30	0.56

¹ Means and standard deviations recorded as per cent values² Compared to control

* 5% level: 2.07

** 1% level: 2.82

changed significantly in their relative proportions at either the 5% or 1% level. These were glycine, threonine, citrulline, tyrosine, at spot 32 which contained valine, norvaline, and methionine. At least three compounds differed significantly at mean dissolved oxygen levels of 1.46 mg/l; namely, glutamic acid, threonine, and spot 35 which may contain phenylalanine, leucine, and isoleucine. At the mean dissolved oxygen level of 0.83 mg/l, seven compounds differed significantly from the control; these were, aspartic acid, glycine, serine, L-alanine, tyrosine, asparagine, and proline. There were no amino nitrogen compounds which differed significantly at all three levels of experimentally lowered dissolved oxygen concentrations; however, glycine, threonine, L-alanine, and tyrosine differed at two of the three dissolved oxygen levels. There were a few amino nitrogen compounds which showed general trends, although they were not significant statistically. Aspartic acid and serine both showed drops in their relative concentrations with a decrease in the amount of dissolved oxygen present.

Salinity experiments: At the 90% salinity level, six spots encompassing ten possible amino nitrogen compounds varied significantly (Table 2). These were glycine, glutamine, l-threonine, tyrosine, spot 32 which may contain valine, norvaline, or methionine, and spot 35 which may contain phenylalanine, leucine, or isoleucine. At 70% level of salinity the concentration of glycine, glutamine, L-alanine, and tyrosine differed significantly from the normal salinity control. An

additional difference was noted in the totals of the optical densities of all ninhydrin-positive spots. The mean optical density values were 2.326 ± 0.766 , 1.036 ± 0.324 , and 1.053 ± 0.300 for normal, 90%, and 70% sea water, respectively. The latter two values differed significantly at the 1% level when compared to the control.

DISCUSSION

The free amino acid pool of *N. arenaceodentata* is somewhat similar, in size and composition, to those free amino acid pools of marine invertebrates which have previously been studied. It is composed of 32 amino acids and related amino nitrogen compounds of which seven account for over 60%. These amino acids are glycine, isoleucine, leucine, phenylalanine, proline, serine, and valine. Simpson, Allen, and Awapara (1959), in their survey of 17 different marine invertebrates, found that glycine, proline, taurine, and three others to a lesser degree, accounted for most of the amino nitrogen present. It was not possible to measure taurine in this study; therefore, no estimation of its presence could be made. Other workers, Camien *et al.* (1951), Kittredge *et al.* (1962), and Clark (1968b) have found similar results in all of the major marine invertebrate phyla.

The free amino acid pool of *N. arenaceodentata* also showed a large amount of variability from one animal to another. Most of the variability was found among the amino acids present in the largest

concentrations. Clark (1968b), and Mearns and Reish (1969) observed similar results in other polychaete species. However, the organisms they studied were from natural field populations. The specimens of *Neanthes arenaceodentata* used in this study were from an inbred population which had been maintained for some 30 generations. Still, a degree of variability remained. To explain this variability other factors were examined. First, the diet of the experimental animal used in this study was controlled. Second, age and maturity were controlled to reduce the possibility of variability introduced by age differences. Third, the environmental factors of temperature, salinity, and light were controlled. Fourth, seasonal variation was controlled by alternating controls and experimentals over a 12 month period. Since all of these factors were held to some degree of constancy, they then can conceivably be given less importance in their role in determining the variability in the free amino acid pool of *N. arenaceodentata*. Perhaps, it is as Clark (1968b) has stated, that under normal conditions, the amino acids in polychaetes are not that closely regulated, and thus vary within a given range.

If the free amino acid pool of *N. arenaceodentata* is compared to the free amino acid pool of the closely related *N. succinea*, the same basic pattern of distribution of amino acids occurs, but differs in relative proportions (Mearns and Reish, 1969). Glycine, L-alanine, glutamic acid, serine, glutamine, and proline accounted for 75% of the free amino acid pool in *N. succinea* but in *N. arenaceodentata* 75% was due to glycine, proline, spot 32 which contains valine, norvaline, or methionine, and spot 35, which contains phenylalanine, leucine, or isoleucine. On the basis of the chromatograms of these two species, *N. arenaceodentata* could easily be distinguished from *N. succinea*. Such comparisons suggest possible phylogenetic relationships which probably exist between these two organisms, and it may indeed be a better method for studying the phylogeny in Family Nereidae than morphological characters (Clark, 1961).

Effects of lowered dissolved oxygen on free amino acids: It is very difficult to assess with certainty the effects of environmental variables on the metabolism of a specific organism. However, the results obtained in this type of study do lend themselves to some general analysis, from which it is possible to make further evaluations. For example, the major changes in relative amounts of amino acids at each level of lowered

dissolved oxygen were the result of changes in a few common amino acids, namely, glycine, isoleucine, leucine, phenylalanine, proline, and serine. These amino acids comprise about 60% of the free amino acid pool. This seems to indicate that the organism is compensating in some way for lowered dissolved oxygen by altering the more abundant amino acids while maintaining constant levels in the majority. This suggests that those amino acids which are maintained at constant levels are most essential for maintenance of normal metabolic activity. Furthermore, the observed fluctuations in free amino acid levels may and probably do reflect degrees of protein synthesis and degradation, induced by lowered dissolved oxygen. Raps and Reish (1971), showed that the polychaete *N. arenaceodentata* increased its hemoglobin levels in order to compensate for lowered dissolved oxygen conditions. R. A. Cripps (pers. comm.) also showed that both protein synthesis and degradation can be induced by lowered dissolved oxygen. If proteins, as stated, are being synthesized and degraded at increased or decreased levels under lowered dissolved oxygen conditions, the free amino acid pool would necessarily fluctuate in accordance with supply and demand for the required amino acids.

A number of amino acids showed a trend in their response to lowered dissolved oxygen. Among these were alanine, aspartic acid, glycine, proline, threonine, and serine. An analysis of the known synthesis and degradation pathways of these amino shows a number of common characteristics which each exhibit, namely:

1. Alanine, aspartic acid, glycine, proline, serine, and threonine, are all closely related and interconnected by their known synthesis and degradation pathways (Mahler and Cordes, 1968), and are essentially interchangeable under different conditions.

2. All except proline are formed by simple one or two step synthesis pathways, making them susceptible to interconversion to other compounds with little or no energy loss (Mahler and Cordes, 1968).

3. All are closely related to carbohydrate metabolism. It is conceivable, therefore, that changes in these amino acids may be the result of stress imposed on the energy production pathways of the organism.

4. All except proline are short chain and simple in structure, hence they are easily formed and are most susceptible to conversion for energy production.

Thus far, all explanations advanced for changes in the free amino acid pool are based on the assumption that under low dissolved oxygen conditions, the organism must compensate in some manner for loss of the terminal electron acceptor, oxygen. If indeed this electron acceptor is oxygen, then without it, alternative means must be taken to insure energy production. Some of these may be behavioral. *Neanthes arenaceodentata* moves to the air-surface interphase under lowered dissolved oxygen condition (Reish, 1967). Other measures may not be as well pronounced as this observed behavior pattern. Compensation by increasing hemoglobin (Raps and Reish, 1971), and increasing enzyme protein or enzyme activity (Simpson and Awapara, 1966; Cripps, pers. comm.), are not well clarified. However, each of these methods of compensation is related to the production of energy; to maintenance of a terminal electron acceptor, or to increased dependence on anaerobic pathways. Changes in the free amino acid levels also are not as distinct as the observed behavior, but appear to be related to compensatory changes in protein metabolism.

Effects of lowered salinity on free amino acids: The most notable change from lower salinities was the decrease in the total concentration of amino acids, which agrees with the earlier findings of Lynch and Wood (1966), Stephens and Virkar (1966), and Clark (1968b). Since the total optical density, hence concentration, of ninhydrin-positive spots was the same at 90 and 70% salinities, it appears as if the free amino acid pool is only regulated to a certain minimum level below which its normal metabolic machinery may be impaired. The 28-day TL_m for *N. arenaceodentata* was about 60% salinity (Reish, 1970) indicating that this impairment of metabolic activity occurred over a long period of time and may have been the cause of death. In short term responses to hyposalinities, Clark (1968a) did not find a stable concentration of amino acids in several species of polychaetes.

Very little is known concerning which amino nitrogen compounds are responsible for the total decreases in concentration. Lynch and Wood (1966) found that proline, glycine, and alanine accounted for most of the responses to lowered salinities in *Crassostrea virginica*. The results with *N. arenaceodentata* suggest that the major adjustment is the result of a general decrease in the size of the pool. Although the increase in percent glycine was significant, the optical density was actually less. The other amino acids decreased in concentration even greater than glycine, giving an

increase in the relative amount of glycine. However, some of the decreases were not significant. At least eight and possibly 12 (counting the multiple of one spot) amino acids decreased in relative proportions at 90% salinity and at least ten and possibly 15 at 70%. However, the glycine concentration remained the same from 90% to 70% salinity. All of these results indicate that the total free amino acid pool is osmotically diluted by decreased salinity and that glycine is maintained at a constant minimum level while the other free amino acids decrease. No explanation is advanced herein to explain this observed glycine stability.

From the results of both the dissolved oxygen and salinity experiments, it is apparent that the free amino acid pool is affected, either directly or indirectly by changes in this organism's environment. Alterations in dissolved oxygen and salinity concentrations accompany some forms of water pollution. Schafer (1961, 1963) has previously noted distinct changes in the free amino acid pool of organisms living in a polluted environment. Therefore, monitoring the effects of these variables on the free amino acid pool may give a measure of how pollution affects some marine organisms.

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AN ANNOTATED KEY TO THE CERCARIAE THAT DEVELOP IN THE SNAIL, *CERITHIDEA CALIFORNICA*

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ABSTRACT: An annotated key is provided to the 18 species of trematodes found in the snail, *Cerithidea californica*; an intermediate host.

Cerithidea californica Haldeman, the California hornshell snail, is common on mud-sand or mud beaches of estuaries and bays of southern California. These areas are favorite feeding grounds for local and migratory shore birds. Bird feces containing trematode eggs result in heavy and varied infections of this snail. The intensity and types of infection vary somewhat with different localities because some regions are more commonly used by birds. Martin (1955) followed the types and infection rates over a one-year period at Newport Bay.

Infected snails are used by biology and zoology classes in the study of larval trematodes. An annotated key to these trematodes should be useful to such studies. Furthermore, the availability of all the stages in a trematode life cycle could be advantageous in physiological and biochemical research.

An attempt was made to keep the key simple, to use distinguishing characteristics that are easily recognized, and that do not require observation with an oil immersion lens, wherever possible.

Cerithidea californica is a favorite host for many trematodes. Eighteen species of cercariae

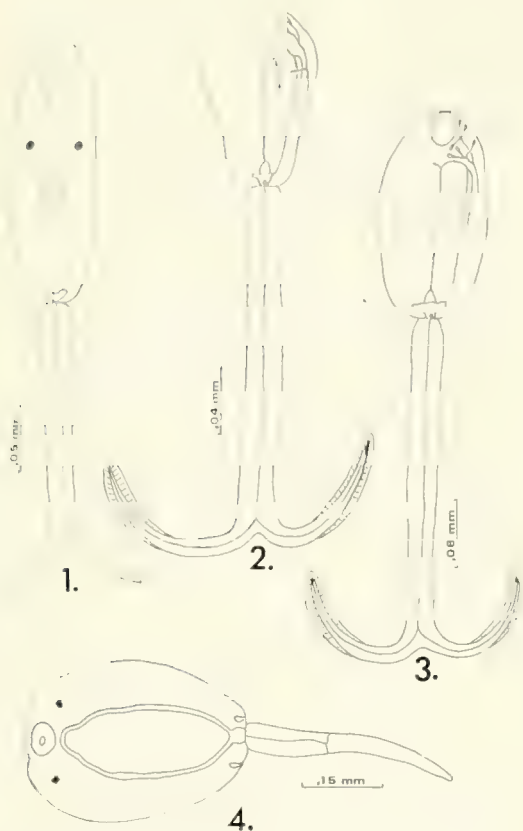
are listed in the following key and it is possible that a few more will be found. Perhaps the cercaria of *Ascocotyle sexidigita* also may use this snail as host. The metacercariae of this species have been found in *Fundulus parvipinnis* living in waters where this snail is common (Martin and Steele, 1970). Judging by the work of Schroeder and Leigh (1965) on the life cycle of *Ascocotyle pachycystis*, the cercaria of *A. sexidigita* should resemble those of *Stictodora* (*Parastictodora*) *hancocki* and *Euhaplorchis californiensis*.

The figures in this paper include only certain details to assist in identification. The size scale is based on fixed specimens; fresh material should be larger. This study was supported by NSF grant GB-6962.

KEY TO CERCARIAE INFECTING *CERITHIDEA CALIFORNICA*

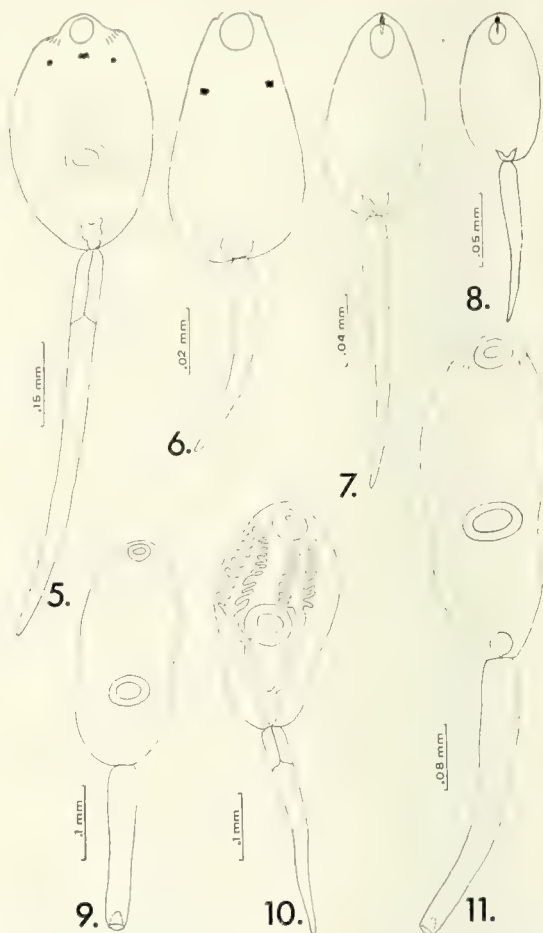
1. a. Tail forked 2
- b. Tail nonforked 4

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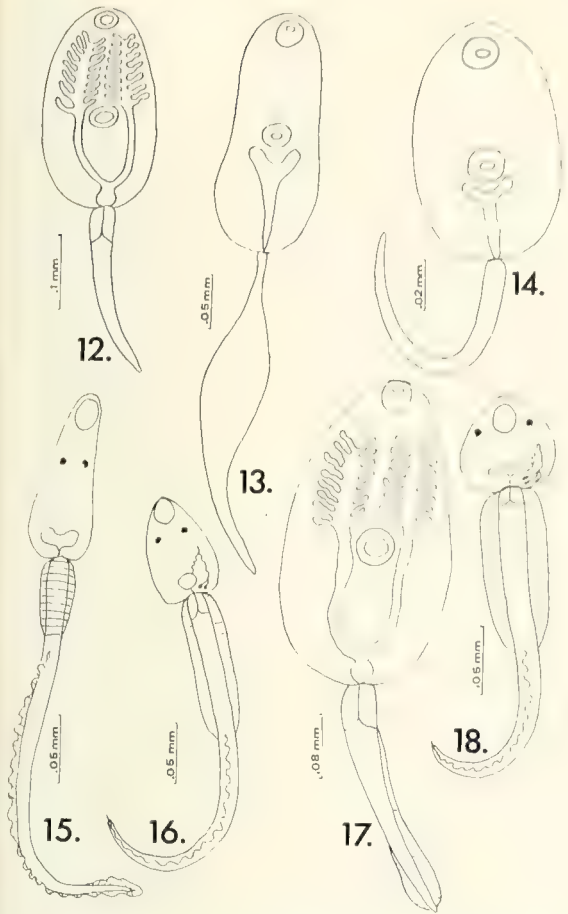
Figures 1-4. 1. Schistosomid. 2, 3. Strigeids. 4. Notocotylid.

2. a. With eyespots—Avian blood fluke. Develops in sporocysts (Fig. 1). This may be the same as *Austrotilharzia penneri* Short and Holliman, 1961 and Holliman (1961) which uses *Cerithidea scalariformis* as intermediate host and chicks, parakeets, and pigeons as experimental adult hosts. However, we have exposed chicks and pigeons to large numbers of the cercaria from *C. californica* with negative results. Therefore this may be a different species of *Austrotilharzia*. Further work is in progress.
- b. Without eyespots 3
3. a. Flame cells in groups of two—Strigeid cercaria (Fig. 2). Develops in sporocysts, cercariae encyst in muscles of *Fundulus parvipinnis*. Life cycle unknown. Smaller than 3b.
- b. Flame cells in groups of three—*Mesostephanus appendiculatus* (Ciurea, 1916) Lutz, 1935 (Fig. 3). Develops in sporocysts, encysts in muscles of *Fundulus parvipinnis*, adults experimentally in intestine of chicks, naturally in shore birds. Life cycle described by Martin (1961).



Figures 5-11. 5, 10. Echinostomids. 6. Heterophyid. 7, 8. Microphallids. 9, 11. Philophthalmids.

4. a. Tail with fins 14
- b. Tail without fins 5
5. a. With eyespots 6
- b. Without eyespots 8
6. a. With a pouch at each posterior-lateral margin of body—*Catantropis johnstoni* Martin, 1956 (Fig. 4). Develops in rediae, encysts on almost any object, adults experimentally in ceca of chicks. Life cycle described by Martin (1956).
- b. Without a pouch at each posterior-lateral margin of body 7
7. a. Encysts in dish—*Himasthla rhigedana* Dietz, 1909 (Fig. 5). Develops in rediae, encysts on almost any object, adults in willet and experimentally in ileum of chick. Life cycle described by Adams and Martin (1963). Cercaria has median pigment spot nearly in line with eyespots.
- b. Does not encyst in dish—*Pygidiosoides*



Figures 12–18. 12, 17. Echinostomids. 13, 14. Renicolids. 15, 16, 18. Heterophyids.

spindalis Martin, 1951 (Fig. 6). Develops in rediae, encysts in gills of *Fundulus parvipinnis*, adults experimentally in intestines of chicks and cats. Life cycle described by Martin (1964).

- 8. a. With stylet (small “spear”) near mouth—Microphallids 1 and 2.
 - 1. Develops in sporocysts (Fig. 7). Larger than 2.
 - 2. Develops in sporocysts (Fig. 8). Smaller than 1.
- Sarkisian (1959) described *Maritrema uca* from fiddler crabs, *Uca crenulata* (Lockington), collected in the same area where the two above microphallid cercariae are found. Apparently one of the above encysts in this crab. Heard and Sikora (1969) placed this species in the genus *Probolocoryphe*.
- b. Without a stylet 9
- 9. a. With pouch opening at end of tail 10
- b. Without pouch opening at end of tail 11

- 10. a. With spined collar—*Parorchis acanthu* (Nicoll, 1906) (Fig. 11). Develops in rediae encysts on almost any object, adults in cloaca of shore birds. Life cycle described by Stunkard and Cable (1932) as *P. avitus* which was declared a synonym of *P. acanthus* by Cable and Martin (1935). I have established infections in chicks by injecting them with metacercariae per cloaca but the percentage of success is low. This cercaria is larger than 10b.
- b. Without spined collar—*Cloacitrema michiganensis* McIntosh, 1938 (Fig. 9). Develops in rediae, encysts on almost any object, adults in cloaca of shore birds. Life cycle outlined by Robinson (1952). I have established infections in chicks by injecting them with metacercariae per cloaca but the percentage of success is low.
- 11. a. With spined collar 12
- b. Without spined collar 13
- 12. a. Encysts in radular muscle—*Acanthoparyphium spinulosum* Johnston, 1917 (Fig. 10). Develops in rediae, encysts in *Cerithidea californica* especially in radular muscles, adults experimentally in intestine of chicks. Life cycle described by Martin and Adams (1960, 1961). Cercaria larger than 12b.
- b. Encysts in feces—*Acanthoparyphium* sp. (Fig. 12). Develops in rediae, encysts in feces of *C. californica* and in certain annelids, adults experimentally in intestine of chicks, Martin and Steele in manuscript.
- 13. a. Usually forms clusters by adhesions of proximal portions of tails, Y-shaped excretory bladder—*Renicola buehanani* (Martin and Gregory, 1951) (Fig. 13). Develops in sporocysts, encysts in liver of *Fundulus parvipinnis*, young adults experimentally in kidneys of *Larus californicus*, Martin (1971). Cercaria larger than 13b.
- b. Does not form clusters, Y-shaped excretory bladder—*Renicola cerithidicola* Martin, 1971 (Fig. 14). Develops in sporocysts, encysts in gills of *Fundulus parvipinnis*, young adults experimentally in kidneys of *Larus californicus*, Martin (1971).
- 14. a. With dorso-ventral tail fin only 15
- b. With dorso-ventral and lateral tail fins 16
- 15. a. With eyespots—*Phocitrema ova* Martin, 1950 (Fig. 15). Develops in rediae, encysts under scales of *Fundulus parvipinnis* and *Atherinopsis californica* (Girard), adults experimentally in chicks and cats. Life cycle described by Martin (1950c).
- b. Without eyespots—*Echinoparyphium* sp. (Fig. 17). Develops in rediae, sometimes forms weak-walled cysts in dish, life cycle unknown.

16. a. Flame cells in groups of twos—*Euhaplorchis californiensis* Martin, 1950 (Fig. 16). Develops in rediae, encysts on brain of *Fundulus parvipinnis*, adults experimentally in small intestines of chicks, *Larus californicus*, cats (Bamberger and Martin, 1951), monkeys, etc. Life cycle described by Martin (1950a).
- b. Flame cells in groups of threes—*Stictodora* (*Parastictodora*) *hancocki* (Martin, 1950) (Fig. 18). Develops in rediae, encysts in various tissues of *Fundulus parvipinnis* and *Gillichthys mirabilis* Cooper, adults experimentally in small intestines of chicks and *Larus californicus*. Life cycle described by Martin (1950b).

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NEW SPECIES OF ROBBER FLIES OF THE GENERA *WILCOXIA* AND *METAPOGON* (DIPTERA: ASILIDAE)

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ABSTRACT: Four new species of the genus *Wilcoxia* are described and a key to the species occurring in southwestern United States and northern Mexico is presented. In addition, two new species of the genus *Metapogon* are described.

The genus *Wilcoxia* has remained monotypic since it was described by James (1941); type species *W. cinerea*. These small robber flies, length 5-10 mm, have the general appearance of *Cophura* Osten Sacken, but lack the twisted spine at the apex of the fore tibiae which is characteristic of that genus. The middle tibiae at the apex has a short straight spine which is usually brown or black. *Wilcoxia* is most closely related to *Metapogon* Coquillett which usually has the mesonotum compressed, highly arched, in lateral view, and with strong anterior dorsocentral bristles, the wings are spotted with brown on the crossveins and furcations, the third vein usually is branched before the end of the discal cell, and the stump vein is long. In *Wilcoxia* the mesonotum is not compressed or highly arched and the strong anterior dorsocentral bristles are absent, the wings are hyaline, uniformly brown, or brownish, the third vein is branched opposite or beyond the end of the discal cell, and the stump vein is usually absent. Wilcox and Martin (1957) presented a key to the related genera. Material received recently for identification has prompted me to describe four new species of *Wilcoxia*.

Measurements were made with an ocular micrometer; the face and wings at 40 $\times$, and the antennae at 75 $\times$.

Wilcoxia martinorum, new species

Description: *Male.* Length 7 mm. Head black, densely grayish white pollinose. Mystax composed of long sparse oral white hairs becoming slightly shorter above and extending to antennae; hairs on frons white; four long and several short bristles on ocellar tubercle and occipitals, yellowish white; beard, hairs on palpi and proboscis white. Face at the antennae 15/28 (.54) width of one eye. Antennae black, grayish pollinose; hairs white; bristles white, two weak bristles below on segment 1 and 2, stronger bristles below on 2; segments 10-8-26-15 in length.

Mesonotum black, densely grayish white pollinose, broadly divided central stripe brown. Sparse hairs white, long erect on humeri and anterior and lateral margins. Bristles yellowish; 2 presutural, 1 supraalar, 1 postalar, 6 dorsocentral (3 anterior). Pleura and coxae densely grayish pollinose, hairs white. Scutellum densely grayish pollinose, sparse discal hairs white, six weak and long yellowish marginal bristles.

Abdomen black, densely gray pollinose with bare spots at middle of tergite 1, 2-6 with an anterior lateral spot on each side and a central posterior spot, and 7 with a small central posterior spot. Hairs white, sparse, long on sides of 1-3; five lateral bristle-like hairs on 1. Sternites gray pollinose, hairs erect white becoming shorter apically. Genitalia brown, parts white.

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Legs black, fore and middle femora dorsally and laterally, hind femora dorsally and sides of apical third, gray pollinose; hairs and bristles white; claws black; empodia and pulvilli, light brown.

Halteres yellow, base brown. Wings hyaline; veins brown; anterior crossvein at 42/60 (.70) length of discal cell; posterior and anal cells open.

Female. Length 7 mm. Frons brownish pollinose. Mesonotum with a spot between humeri and central stripe and the anterior intermediate spots, golden brown pollinose. Abdominal segments 7-8 brownish black and bare of pollen, apical spines brown. Wings with a faint brown clouding on the crossveins and furcations.

Holotype: male, California, Riverside Co., White Water, 23 December 1947 (J. Wilcox) CAS. *Allotype:* female, same data as holotype.

Named in honor of the ardent collecting team of Dorothy and Charles H. Martin who found this species literally swarming on the hillside rocks near the entrance to White Water Canyon on 23 December 1947.

Prey: A small anthomyiid fly, two borboid flies and a small green hymenopteran were taken by P. H. Arnaud, Jr. and a small winged termite by A. L. Melander.

Other specimens examined: ARIZONA. *Maricopa Co.*, ♂, 21 mi N Ajo, 11 November 1966 (R. J. Hamton) EF; *Pima Co.*, 8♂, 7♀, Organ Pipe Cactus National Monument, 2 mi N Headquarters, 11 November 1966 (R. J. Hamton) EF; *Yuma Co.*, 8♂, 12♀, Brenda, 28 October 1967 (S. A. Gorodenski and M. A. Cazier) ASU. CALIFORNIA. *Imperial Co.*, ♀, Painted Gorge, Coyote Mts., 22 August 1934 (C. D. Michener) CIS; *Inyo Co.*, ♂, Death Valley National Monument, 1.5 mi SW Wildrose Station, 3100 ft, 6 November 1968 (P. H. Arnaud, Jr.) at flowers of *Chrysothamnus peniculatus* (Gray) Hall, CAS; *Riverside Co.*, ♀, Coyote Creek, 6 November 1963 (E. I. Schlinger) UCR; 5♂, 2♀, Deep Canyon, P. S. Boyd Desert Research Center, 3.5 mi S Palm Desert, marker no. 57, 6 November to 22 December 1963, 1969, 31 January to 10 February 1970 (S. Frommer, M. E. Irwin, L. La Pre, E. I. Schlinger, and R. Worley) at light and malaise trap, UCR; ♀, Desert Hot Springs, Los Angeles Aqueduct, 25 January 1947 (G. H. Sperry and J. L. Sperry) USNM; 4♂, 7♀, Joshua Tree National Monument (JTNM); Pleasant Valley, Fried Liver Wash, 22 October 1967, 29 October 1965 (E. L. Sleeper) part blacklight, CSCLB; 6♂, 10♀, 5 and 10 mi S Oasis, 17 November 1947, 10 December 1962 (A. F. Howland, I. J. Wilcox, and J. Wilcox) JW; 2♂, Palm Desert, 10 October 1964 (E. Fisher) EF; 4♂, 3♀, Palm Springs, 12 November 1944, 19 November 1943 (A. L. Melander) USNM; 77♂, 73♀, Palm Springs, 23 December 1950, 29 December 1953 to 8 January 1954, 21 January 1953 (P. H. Arnaud, Jr.) JW; 5♂, 2♀, Palm Springs, 21 January 1953, 16 December 1964 (M. W. Stone and J. Wilcox) JW; 9♂, 13♀, Palm Springs, Chino Canyon, 22 to 26

December 1950 (P. H. Arnaud, Jr.) JW; 5♂, 17♀, Palm Springs, Tahquitz Canyon, 24 November 1944 (A. L. Melander) USNM; 46♂, 135♀, White Water, 23 November to 27 December 1947, 6 January 1948 (A. F. Howland, C. H. Martin, D. Martin, I. J. Wilcox, and J. Wilcox) CHM, CIS, JW, UCD; 15♂, 12♀, White Water, 11 November 1966, 13 November, 16 December 1962 (E. Fisher and R. J. Hamton) EF. NEVADA. *Nye Co.*, ♂, Rhyolite, 2 October 1936 (A. J. Basinger) CAS. MEXICO. *Sonora*, 3♂, 2♀, 13 mi SW Sonoyta, 12 November 1966 (E. Fisher) EF.

Wilcoxia monae, new species

Description: *Male.* Length 6 mm. Head black, densely whitish pollinose. Mystax white, composed of weak oral bristles and hairs above about half as long; hairs on frons white; six short erect bristles on ocellar tubercle and occipitals, yellowish; beard, hairs on palpi and proboscis white. Face at antennae 20/24 (.83) width of one eye. Antennae black, hairs white, segment 2 with two longer hairs below; segments 11-11-40-12 in length.

Mesonotum black, gray pollinose, broadly divided central stripe brown. Hairs white, appressed and as long as antennae 1. Bristles yellowish, 4 presutural, 3 supraalar, 3 postalar, 4 posterior dorsocentral. Pleura and coxae gray pollinose, hairs white. Disc of scutellum gray pollinose with short sparse white hairs, broad posterior margin black with four weak, yellowish bristles.

Abdomen shining black, sides of tergites 1-6, slightly projecting inward on posterior margins of 4-6, gray pollinose. Hairs short yellowish white, sparse on dorsum; three or four yellowish lateral bristles on 1. Sternites gray pollinose, hairs erect white, dense apically. Genitalia brown, hairs yellowish.

Femora black, narrow base and about apical third yellowish-red; tibiae and tarsi yellowish-red; fore tarsi and segment 5 of middle and hind tarsi brown. Hairs white; bristles yellowish; claws black; empodia white; pulvilli gray.

Halteres yellow, base brown. Wings brown with lighter spots in posterior cells; veins brown, anterior crossvein at 38/59 (.64) length of discal cell; third vein branched beyond end of discal cell; all posterior cells and anal cell narrowly, open.

Female. Length 7 mm. Oral bristles yellowish. Dorsum of abdominal tergite 6, all of 7-8, and apical spines brown. Wings light yellowish brown, anterior crossvein at 45/67 (.67) length of discal cell. Anterior side of fore tibiae and all tarsi brownish black.

Holotype: male, California, Mono Co., Mammoth, 9 August 1957 (J. Wilcox) CAS. *Allotype:* female, same data as holotype.

Other specimens examined: CALIFORNIA. *Mono Co.*, 26♂, 4♀, Mammoth, 9 August 1957 (I. J. Wilcox and J. Wilcox) EF, JW; *Nevada Co.*, ♀, 3 mi N

Boca, 23 July 1961 (F. D. Parker) UCD; ♀, 1 mi S Hobart Mills, 1 September 1957 (E. G. Linsley) *Chrysothamnus viscidiflorus* var. *typicus*, CIS; ♂, Prosser Dam, 15 July 1966 (D. R. Miller) UCD; ♂, 2 ♀, Truckee, 17 August 1955 (E. G. Linsley) Compositae, CIS; *Tulare Co.*, ♀, Mineral King, 8 August 1959 (W. E. Simonds) CDA; ♂, ♀, 0.5 mi E Smith Meadow, Nine Mile Canyon, 7850 ft, 5 August 1961 (C. W. O'Brien) CIS. NEVADA. *Douglas Co.*, ♂, Topaz Lake, 17 August 1960 (A. S. Menke) UCD.

***Wilcoxia painteri*, new species**

Description: Male. Length 5 mm. Head black densely whitish pollinose, frons with central golden spot. Hairs white, lower third of mystax long, short and sparse above; occipital and four erect bristles on ocellar tubercle white. Face at antennae 16/19 (.84) width of one eye. Antennae brownish black; hairs white; segment 2 with one weak white bristle below; 3 nearly uniform in width and style broad; segments 7-8-25-10 in length.

Mesonotum black; grayish pollinose, divided central stripe, anterior and posterior intermediate spots and a small spot opposite postalar calli, brown pollinose. Short sparse hairs white. Bristles yellowish, 2 weak humeral, 2 presutural, 2 supraalar, 1 postalar, 4 dorsocentral (1 anterior). Pleura and coxae grayish pollinose, hairs white. Scutellum grayish pollinose, two erect marginal bristles yellowish, fine marginal hairs white.

Abdomen brownish black; narrow lateral margins of all tergites and very narrow anterior margin of 2-6, gray pollinose. Fine hairs white, longer laterally on 1-3; three yellowish lateral bristles on 1. Sternites grayish pollinose, narrow central line bare of pollen, hairs white. Genitalia small and black, hairs white.

Femora except tips, apices of tibiae and tarsal segments black; tips of femora, basal part of tibiae and tarsi, yellowish-red. Hairs and bristles white; claws black, reddish basally; pulvilli brown.

Halteres yellowish, base of stem brownish. Wings hyaline, veins light brown, anterior crossvein at 28/46 (.61) length of discal cell; third vein branched opposite end of discal cell; all posterior and anal cells open.

Female. Length 6 mm. Intermediate spots of mesonotum bare of pollen and shining brownish-black. Anterior fascia on abdomen slightly broader, and absent on tergite 6; apical spines black. Third vein branched slightly beyond end of discal cell and in one wing with minute stump vein.

Holotype: male, New Mexico, Catron Co., Datil, Continental Divide, 17 July 1930 (T. F. Winburn and R. H. Painter) RHP. *Allotype:* female, same data as holotype.

Named in honor of the late Reginald H. Painter who, although not especially interested in Asilidae,

always collected rare and interesting species on many trips.

Other specimens examined: NEW MEXICO. *Catron Co.*, ♂, 2 ♀. Datil, Continental Divide, 17 July 1930 (T. F. Winburn and R. H. Painter) RHP, JW. ARIZONA. *Apache Co.*, ♀, Chino Lee (Chinle), 26 July 1935 (Brues) USNM. UTAH. *Kane Co.*, ♀, 16 mi W Glen Canyon, 23 September 1969 (P. H. Timberlake) *Sutienzia* sp., UCR; *Millard Co.*, ♂, 23 mi W Delta, 4900 ft, 4 September 1965 (R. H. Painter and E. M. Painter) RHP; *Uintah Co.*, ♀, 16 mi SW Vernal, 5000 ft, 7 September 1965 (R. H. Painter and E. M. Painter) RHP; county undetermined, ♀, Showell, 20 August 1932 (G. F. Knowlton) JW, [anterior fascia on abdomen of this specimen much broader and faint fascia on tergite 6].

***Wilcoxia pollinosa*, new species**

Description: Male. Length 8 mm. Head black, densely white pollinose. Hairs and bristles white; mystax of about eight oral bristles and short hairs extending half way to antennae; two erect bristles on ocellar tubercle. Face at antennae 17/23 (.74) width of one eye. Antennae black; short sparse hairs white; one weak white bristle below on segment 1 and one strong below on 2; segments 9-10-29-14 in length.

Mesonotum black; white pollinose, divided central stripe and small intermediate spots brown. Hairs short sparse semierect white. Bristles white, 2 presutural, 1 supraalar, 1 postalar, 4 weak, anterior dorsocentral (pin obscures posterior ones). Pleura and coxae black; white pollinose; hairs white, short on coxae, long on hypopleura. Scutellum black; white pollinose; three strong white marginal bristles.

Abdomen black; tergites 1-8 white pollinose, small central and lateral bare spots on 2-6. Hairs short white, recumbent on dorsum, semierect on sides; five white lateral bristles on 1 plus a few longer hairs. Sternites grayish white pollinose, hairs short semierect white. Genitalia yellowish-red basally, brown apically; hairs long and white.

Femora and tibiae yellowish-red; apical half of fore femora, apical fourth of middle and hind femora, and apical fifth of all tibiae, black; tarsi black. Hairs and bristles white; claws black, base reddish; pulvilli and empodia yellowish-red.

Halteres yellowish, lower stem light brown. Wings hyaline; veins brown; anterior crossvein at 36/57 (.63) length of discal cell; third vein branched slightly beyond end of discal cell; posterior cells broadly open; anal cell narrowly open.

Female. Length 10 mm. Weak bristle below on antennal segment 2. Mesonotal pollen with a yellowish cast; two posterior and four anterior central bristles; two scutellar bristles. Abdomen segments 1-6 and 7 basally, grayish pollinose, 8 terminalia and spines reddish-brown, hairs yellowish

Hairs and bristles of legs white to yellowish. Anterior crossvein at 50/76 (.66) length of discal cell; third vein branched opposite end of discal cell.

Holotype: male, New Mexico, Chaves Co., 6 mi W Roswell, 15 September 1965 (P. H. Timberlake) UCR. *Allotype*: female, New Mexico, Eddy Co., 0.5 mi N State Line, Hwy. 180 and 62, 2 October 1962 (C. S. Papp) UCR.

Other specimens examined: NEW MEXICO. Eddy Co., ♀, 16 mi S Artesia, 3000–3500 ft, 24 September 1950 (W. Gertsch and M. Cazier) AMNH [thorax and abdomen greased, ground color black except posterior lateral margins, and postalar calli of mesonotum reddish; 3 scutellar bristles]; *Torrance Co.*, ♀, Gran Quivira, 11 August 1931 (R. H. Painter) RHP [third antennal segment missing and scutellum crushed]. TEXAS. *Hudspeth Co.*, ♀, 30 August 1940 (D. J. Knull and J. N. Knull) OSU.

KEY TO THE SPECIES OF *WILCOXIA*

1. Posterior margin of the scutellum bare of pollen; wings of the males brown, females lighter brown; abdomen black, lateral margins gray pollinose somewhat expanded apically on the tergites 2

Scutellum all pollinose; wings hyaline; abdomen with at least some pollen on the dorsum of the tergites 3

2. Legs black, basal fourth of fore, middle, and basal half of hind tibiae bright yellow, apices of fore and hind femora yellow; mesonotum gray pollinose, divided central stripe black, and small anterior intermediate spots brown; length 6.5–7.0 mm (Colorado) *cinerea* James

Legs yellowish-red, basal two-thirds of femora, except extreme base, black; mesonotum densely gray pollinose, divided central stripe indistinctly brown; length 6–7 mm (California and Nevada) *monae* Wilcox

3. Legs black, femora largely white pollinose and only the tips reddish; abdomen white pollinose, central part of tergite 1, large central posterior spot and small lateral anterior spots on 2–6, bare of pollen; length 6–7 mm (California, Arizona, and Nevada)

..... *martinorum* Wilcox

At least the tibiae largely yellowish or reddish ... 4

4. Femora except tips, tips of tibiae, and tips of tarsal segments brown or black, tips of femora, and basal part to tibiae and tarsi reddish; abdomen black, narrow lateral margins of tergites 1–6, narrow anterior margins of male 2–6 and female 2–5, gray pollinose; length 5–6 mm (Arizona, New Mexico, and Utah) *painteri* Wilcox

Femora except apical fourth and tibiae except

tips, yellowish-red, apex of femora and tibiae, and all of tarsi, brown or black; abdomen black, densely gray pollinose, tergites 2–6 with small lateral bare spots; length 8–11 mm (New Mexico and Texas) *pollinosa* Wilcox

Metapogon amargosae, new species

Description: *Male*. Length 8 mm. Head black, white pollinose, hairs and bristles white. Face at antennae 22/28 (.79) width of one eye. Antennae black, grayish pollinose; hairs white, segments 1–2 each with a white bristle below; segments 10–10.35–19 in length.

Mesonotum black; grayish white pollinose; broadly divided central stripe, small intermediate spots, and dorsocentral stripes broad anteriorly, brown. Hairs erect, white, and subequal in length to antennae 1–2. Bristles white, 2–3 presutural, 1 supraalar, 1 postalar; bristles brown, four anterior and four posterior dorso-central and 12 anterior on the central stripe. Pleura and coxae grayish pollinose, hairs white. Scutellum white pollinose with a round central bare spot, hairs white, two strong, brown and two weak, pale marginal bristles.

Abdomen black; sides of tergites 1–3, anterior margins of 2–7 and posterior corners of 2–6 extending narrowly inward on posterior margins of 2–4 (entire on 4), grayish-white pollinose. Hairs and bristles white, long on sides of 1–3. Sternites grayish pollinose, 2–6 with small lateral bare spots, and a median, apical, triangular brownish spot, hairs white. Genitalia small, black, hairs white.

Legs black, tips of femora and dorsum of tibiae brown. Hairs and bristles white; claws black, base reddish; empodia and pulvilli whitish, pulvilli 4/5 length of claws.

Halteres yellowish, base and lower part of knob brown. Wings hyaline with small, brown spots on the crossveins and furcation; veins brown; anterior crossvein at 43/68 (.63) length of discal cell; third vein branched before end of discal cell and with short stump vein.

Female. Length 9 mm. One weak, pale scutellar bristle (others probably broken off). Anterior fascia and posterior pollinose spots on abdominal tergites 4–6 connected, 7 largely pollinose dorsally.

Holotype: male, Nevada, Nye Co., 2 mi S Beatty, 24 December 1964 (D. L. Coates) UI (CAS). *Allotype*: female same data, as holotype.

This species runs to couplet 4 in the key to the species (Wilcox, 1964). In *Metapogon pictus* Cole and *M. tricellus* Wilcox the white hairs anteriorly on the central stripe are subequal in length to antennal segment 1, and there are no bristles on the anterior central stripe. In *M. gibber* (Williston) and *M. carinatus* Wilcox, the anterior hairs on the central stripe are usually black, but a few *M. carinatus* have white hairs; in *M. gibber* there are no anterior bristles

on the central stripe whereas, *M. carinatus* has about 30 black bristles.

Other specimens examined: NEVADA. Nye Co., 2 ♂, 2 mi S Beatty, 24 December 1964 (D. L. Coates) UI, JW. ARIZONA. Maricopa Co., ♀, Tempe, 21 November 1967 (D. Plantz) ASU. CALIFORNIA. Riverside Co., ♀, Blythe, 28 October 1940 (K. S. Snyder) Tamarix, CIS; San Bernardino Co., ♂, ♀, Needles, 20 March 1967 (R. M. Bohart and D. S. Horning, Jr.) UCD; 6 ♂, 3 ♀, Twentynine Palms, 23 October, 6 November 1967 (E. Fisher) EF, [taken resting on the foliage of low shrubs on the sand dunes near the golf course about 2 miles northeast of town].

Metapogon obispae, new species

Description: Male. Length 5 mm. Head black; grayish pollinose with a golden tinge on face, and central frons brown. Mystax with six brown oral and six black bristles above, plus a few short brown and black hairs; 3–4 short, black hairs on sides of frons; four strong, erect black bristles on ocellar tubercle; short occipital bristles black above and brown below; sparse beard and hairs on palpi and proboscis white. Face at antennae 18/22 (.82) width of one eye. Antennae black; short sparse hairs, and one bristle below on segment 1, black; segment 3 broader beyond middle; segments 9–9–30–9 in length.

Mesonotum black; central stripe and intermediate spots dark brown, lateral margins golden brown, area between central stripe and intermediate spots, and a narrow median line, silvery pollinose. Sparse hairs black and subequal in length to antennae 1. Bristles black, 2 presutural, 1 supraalar, 1 postalar, 1 weak posterior and three strong anterior dorsocentral. Pleura and coxae black, grayish-brown pollinose; short hairs on coxae white; 5–6 long hypopleurals black. Scutellum black; silvery pollinose with golden tinge; four strong, black marginal bristles.

Abdomen black; grayish pollinose with golden tinge, at some angles lateral, anterior black spots are apparent on tergites 2–5 and small round central spots on 2–6. Hairs short, sparse, recumbent, and black, white laterally with a few longer hairs on 1–2; four to five brown lateral bristles on 1. Sternites black, grayish-golden pollinose, short, sparse erect hairs white. Genitalia black, hairs white.

Legs black, tips of femora and dorsum of tibiae dark reddish; hairs white; bristles brown; claws black; pulvilli dark brown, 4/5 length of claws; empodia brown.

Halteres yellow, stem brown. Wings light brown, the brown intensified on the crossveins, furcations, and apex; veins black; anterior crossvein at 31/45 (.69) length of discal cell; third vein branched slightly before end of discal cell and with long stump vein; posterior cells broadly open; anal cell narrowly open.

Female. Length 6 mm. Median line of mesonotum golden. Abdominal segments 1–7 grayish pollinose, 8 shining black; apical spines black, short hairs white.

Holotype: male, California, San Luis Obispo Co., Baywood Park, 24 October 1970 (J. Wilcox) CAS. *Allotype:* female, same data as holotype, 25 October 1970.

In the key to the species (Wilcox, 1964) this species runs to couplet 10; with its long pulvilli it would be close to *M. tarsalis* Wilcox from which it differs by having the abdomen all pollinose and is without bare spots on the mesonotum.

Other specimens examined: CALIFORNIA. San Luis Obispo Co., 41 ♂, 28 ♀, Baywood Park, 23 to 25 October 1970 (J. Wilcox) CAS. [collected on the ground and low weeds on the dunes overgrown with trees, brush, and weeds about two miles east of Morro Bay (Baywood Park P.O.) near the intersection of Nipomo Ave. and Willow Drive].

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RESEARCH NOTES

A FIRST REPORT OF SELF-FERTILIZATION IN THE WOOD-BORING FAMILY TEREDINIDAE (MOLLUSCA: BIVALVIA)

Three mechanisms for fertilization have been recognized in the family Teredinidae: (1) Sex products are released into sea water where fertilization occurs as in *Teredo* (*Nototeredo*) *norvagica* (Lebour, 1938, 1946; Nair, 1962), *Teredo* (*Psiloteredo*) *megotara* (Sigerfoos, 1908; Nair, 1962), *Bankia setacea* (Coe, 1941; Quayle, 1953), *B. indica* (Nair, 1956a, b), *Nausitora dunlopei* (Smith, 1963), *B. australis* (Turner, 1971), and perhaps *B. gouldi* (Sigerfoos, 1908). (2) Sperm is released into sea water by the male and drawn into the incurrent siphon of a neighboring female where fertilization occurs in the mantle cavity as in *Lyrodus pedicellatus* (Roch, 1940; Becker, 1959), *L. diegensis* (= *pedicellatus*) (Kofoid and Miller, 1927), *L. medilobata* (Edmonson, 1942), *Teredo navalis* (Grave, 1928), *T. poculifer* (Smith, 1963), and *L. pedicellatus* (cf. *T. bartschi*) (Isham and Tierney, 1953). Turner (1966) also reported *T. furcifera*, *T. parksi* (= sexually mature but small, young *T. furcifera*, Turner, 1966), *T. somersi*, *T. clappi*, *L. affinis*, and *L. massa* with brooded young from test panels, which proved that fertilization had occurred in the epibranchial cavities in these species. (3) Sperm possibly being transferred from one male to a neighboring female by the insertion of the male excurrent siphon into the female incurrent siphon as observed by Clapp (1951) in *Bankia gouldi* and by Townsley, Richy, and Trussell (1966) in *B. setacea*.

No report of self-fertilization in the family has been made although Coe (1941) demonstrated that the sexual phases in *Lyrodus* and *Teredo* were not sharply demarcated and functional hermaphroditism in which the male and female stages occurred simultaneously was common. However, there has been no laboratory evidence to suggest that self-fertilization in brooding forms is indeed a fact.

During laboratory studies on the effects of temperature and reduced salinity on larvae and adults of *L. pedicellatus* (Eckelbarger and Reish, 1972), adults isolated from the veliger stage to an age of five months produced apparently normal veligers. Although the purpose of the experiment was to assess the effects of temperature and reduced salinity on growth and survival, the fact that all test animals were completely isolated, one per flask from the pediveliger stage, yet produced larvae proves the existence of a mechanism for self-fertilization in this species.

METHODS

Lyrodus pedicellatus larvae were obtained by placing infested wood blocks brought from the field in room temperature sea water as a stimulant for the release of larvae. Actively swimming pediveligers were pipetted individually into separate petri dishes containing 75 ml of normal chlorinity (19.2 ‰) sea water and a presoaked block of Douglas fir measuring 5 × 25 × 42 mm. All dishes were left undisturbed for a week in reduced light at room temperature. Only those boring larvae with normally appearing calcareous caps and visible siphons were selected for the experiment.

A series of eight concentrations of sea water was prepared by dilution with appropriate volumes of distilled water; these included 19.3, 16.0, 13.0, 11.0, 9.0, 7.0, 5.0, and 3.0 ‰. Chlorinities were determined by titration with silver nitrate (Barnes, 1959). A wood block containing one *Lyrodus* was placed in each of ten 500 ml erlenmeyer flasks with 100 ml of sea water at each chlorinity level. The flasks were sealed with a number seven rubber stopper. The experiment was conducted at two temperatures, one at room temperature (22–24 °C) and the second at 14–16 °C. Each wood block was removed from its flask and examined weekly under a dissection microscope. Observations were noted on the appearance of the pallets, the calcareous cap, and the behavior of the animal. The blocks were then returned to the flasks with fresh filtered sea water. At no time was sea water from one flask transferred to another in order to prevent the exchange of sperm between organisms.

The experiment was terminated at the end of 5 months at which time all animals were removed from their blocks. The mantle cavity and gill filaments were examined for the presence of mature veligers and were counted if present.

RESULTS

Table 1 indicates that larvae were found in 40, 25, and 11% of the animals in chlorinities of 19.3, 16.0, and 13.0 ‰, respectively, at 14–16 °C. Larvae were found in 30 and 20% of the animals at 19.3 and 16.0 ‰, respectively, at 22–24 °C. Animals raised at 14–16 °C contained 49 larvae as compared to 25 at 22–24 °C.

DISCUSSION

Protandry in teredinids was proved by Yonge (1926) from histological work on *Teredo* (*Nototeredo*) *norvagica* although it had been earlier postulated by Sigerfoos (1908) in *Bankia gouldi*. Coe (1933–41)

TABLE 1. The effects of temperature and reduced chlorinity on survival and reproduction of *Lyrodus pedicellatus*.

Chlorinity (%)	No. of Surviving Test Animals	No. With Veligers	No. of Surviving Test Animals	No. With Veligers
	14-16 C		22-24 C	
19.3	10	4	10	3
16.0	8	2	10	2
13.0	9	1	8	0
11.0	4	0	4	0
9.0	0	0	1	0

found *Teredo navalis*, *B. setacea*, and *L. diegensis* (= *L. pedicellatus*) all to be protandrous hermaphrodites. He found the sexual phases not sharply demarcated in *L. diegensis*, and was able to achieve artificial fertilization and development through gastrulation. In the experiments presented herein, direct evidence is given proving that at least one species of teredinid is capable of self-fertilization.

The reduction in animals producing larvae at lower chlorinity levels was an expected result since the species is sensitive to reduced chlorinities (Eckelbarger and Reish, 1972). Kinne (1963) confirmed that embryonic and larval stages are almost universally more sensitive than adults of the same species.

The greater number of larvae produced at the lower temperature level may reflect a lower sensitivity to reduced chlorinity conditions as a result of the lower temperature. It maybe that there is increased maternal retention of larvae at lower temperatures. Coe (1941) stated that this species could retain its larvae within the maternal gill for several months until more favorable temperatures. Since the 14-16 C range corresponded to the seasonal low reported by Moore and Reish (1969) for Alamitos Bay, Long Beach, and for Los Angeles-Long Beach Harbors by Menzies, Mohr, and Wakeman (1963), it is possible that the higher larval count reflected this maternal retention.

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RHADINAEA GODMANI, AN ADDITION TO THE SNAKE FAUNA OF HONDURAS

Rhadinaea godmani (Günther) has been recorded from Guatemala (Slevin, 1939; Stuart, 1951, 1963), El Salvador (Mertens, 1952a, 1952b; Uzzell and Starrett, 1958), and Costa Rica (Scott, 1969). Recent field work by us has revealed its presence in Honduras. On the afternoon of 9 April 1971 we secured one male specimen (LSUMZ 24398) from underneath a rock near a log slide at an elevation of 1740 m in *Pinus pseudostrobus* forest (pinabetal of Carr, 1950; Lower Montane Moist Forest formation of Holdridge, 1962) on Cerro Uyuca, Depto. de Francisco Morazán. On 29 April 1971 an additional specimen (LACM 72070) was found by Eric and Susan Festin at an elevation of 1450 m in *Pinus oocarpa* forest (ocotal of Carr, 1950; Subtropical Moist Forest formation of Holdridge, 1962) at El Hatillo, Depto. Francisco Morazán.

Both specimens are males exhibiting the following measurements and features of scutellation (data for LSUMZ 24398 listed first): ventrals 159, 156; subcaudals 92, 92; supralabials 8-8 in both; infralabials 9-9 in both; dorsal scale rows 19-21-21 in both; total length 405, 407 mm; tail length 122, 129. Other scutellational data are typical for the species.

In life LACM 72070 exhibited the following color and pattern; rows 1 through 3 yellowish-orange, adjacent portions of rows 1 and 2 and rows 2 and 3 with black flecking giving impression of narrow, diffuse stripes; lower portion of row 4 light yellow; upper portion of row 4, most of row 5, and lower portion of row 6 black; upper portion of row 6 and lower edge of row 7 light yellow; ground color of upper two-thirds of row 7 through row 10 medium brown, edges of these scales black giving impression of narrow, irregular, diffuse stripes on adjacent portions of scale rows; middorsal row black lightly mottled with brown.

Dorsum of head dark brown with faint light yellow mottling and a tiny, but distinct, light yellow dot in middle of each parietal; light yellow band across snout on posterior portion of rostral and anterior portion of internasals, in connection with light pigment

on supralabials; supralabials mostly ivory, supralabials 1 through 4 with dark brown upper and lower edges, dark blotch on upper portion of supralabial 6 extending diagonally across lower portion of supralabial 6, upper edge of supralabial 6, upper half of 7, and all but anteroventral corner of 8 dark brown (the dark diagonal subocular blotch and the dark pigment on supralabials 6 through 8 appear to outline a pale diagonal stripe from eye to lip); infralabials ivory with dark brown mottling on anterior ones; chin ivory; iris dark brown. The other specimen (LSUMZ 24398) agrees in essential aspects with the above description.

Keels are present on the dorsal scales above the vent in LACM 72070 but not in LSUMZ 24398. Mertens (1952a) described *Rhadinaea zilchi* on the basis of a single specimen from El Salvador, distinguishing this taxon from *Rhadinaea godmani* on the basis of differences in dorsal color pattern and the presence of supra-anal keels in the former. In a later paper Mertens (1952b) pointed out that there was actually no difference in color pattern between *godmani* and *zilchi*. The differences given in the original description of *zilchi* were based on an error in the pattern representation of *godmani* given by Stuart and Bailey (1941), an error later corrected by Stuart (1951). Mertens (1952b) suggested that since the presence of supra-anal keels in *zilchi* and their absence in *godmani* served to distinguish the two, that *zilchi* be regarded as a subspecies of *godmani*. Two additional adult male *R. godmani* (from El Salvador) discussed by Uzzell and Starrett (1958), possess well-developed supra-anal keels, whereas, a topotypic Guatemalan specimen of the nominate subspecies has supra-anal keels that are less well-developed. They suggested that the differences between *godmani* and *zilchi* "seem too slight to be of taxonomic importance." However, Merten's view was accepted by Peters and Orejas-Miranda (1970) along with the erroneous conception that pattern differences exist between the two. Inasmuch as the name *zilchi* is based upon only two specimens and the character of supra-anal keeling appears to vary intrapopulationally, we suggest that *Rhadinaea zilchi* Mertens be regarded as a synonym of *Rhadinaea godmani* (Günther) 1865.

Scott (1969) recorded *Rhadinaea godmani* from several localities in Costa Rica, apparently the first records for the species in that country. Taylor (1951, 1954) did not list *R. godmani* as a member of the Costa Rican snake fauna, but he (Taylor, 1954) did describe a new species, *Rhadinaea altamontana*, on the basis of one specimen from the Cordillera de Talamanca in Costa Rica. In this paper, he regarded *altamontana* as most closely related to *godmani* but stated that the two could be distinguished on the basis of differences in color pattern, head length, and supra-anal keeling (keels present in *altamontana*, keels not present in *godmani*). We have not examined the holotype of *altamontana* but we discount the impor-

tance of supra-anal keeling and point out that the description of the color pattern of the holotype is very similar (but not identical, according to Taylor's description) to the color pattern of *godmani*. This suggests that *Rhadinaea altamontana* Taylor is probably a synonym of *R. godmani* and thus support the implication of Scott (1969) that *altamontana* is not recognizable.

Presently, *Rhadinaea godmani* is known to occur at moderate and intermediate elevations (1450–2660 m) of both versants from southwestern Guatemala to Costa Rica; it has thus far not been recorded from Nicaragua.

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A NEW SPECIES OF *BAETODES* FROM ARIZONA (EPHEMEROPTERA: BAETIDAE)

The first record of *Baetodes* in North America, north of Mexico, was reported by Edmunds (Ent. News, 61:203-205, 1950) from nymphs collected by J. G. Needham in the Rio Frio, Garner State Park, Uvalde Co., Texas. An assemblage of mayfly nymphs from Arizona were found to belong to an undescribed species of *Baetodes*, representing the second record of the genus for North America, north of Mexico. The holotype is deposited in the California Academy of Sciences. We thank Jerry Battagliotti for preparing the included figures. The research upon which this report is based was supported by the National Science Foundation.

Baetodes sigillatus, new species

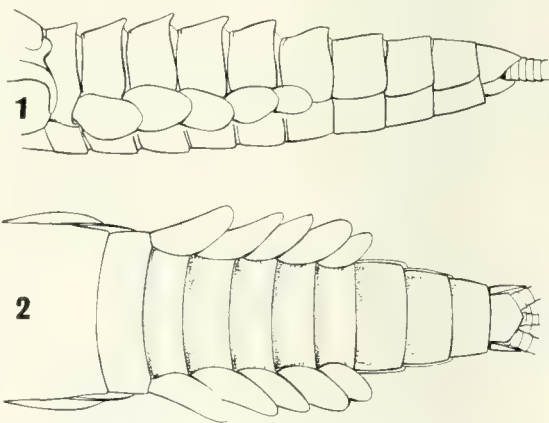
Figures 1 and 2

Description: *Nymph*.—Length: body 5.0-6.0 mm; caudal filaments 4.0-5.0 mm. General color light brown with reddish-brown markings. Head light brown with brown and reddish-brown markings; occiput brown, frons and genae reddish-brown; head without setae. Thoracic nota light brown with brown and reddish-brown markings; pronotum light brown with intricate brown and reddish-brown markings; mesonotum light brown with reddish-brown anterior transverse band, and with submedian longitudinal brown streaks; pronotum with a dorsal, median, posterior elevation; mesonotum without a dorsal elevation; thoracic nota without setae; thoracic sterna pale; legs light brown to brown with reddish-brown markings; femora light brown often margined with

reddish-brown; tibiae brown; tarsi brown to dark brown; coxae without gills; tarsal claws with 6-7 denticles. Abdominal terga light brown with reddish-brown markings; abdominal terga 1-9 with a reddish-brown transverse band; abdominal terga 6-10 with a median pale stripe, and often with submedian pale spots; abdominal tergum 10 light brown; abdominal terga 1-6 with small median tubercles, tubercle on tergum 6 barely discernable (Fig. 1); abdominal terga without setae; abdominal gills pale; abdominal sterna light brown with reddish brown markings; abdominal sterna 1-7 with an anterior transverse reddish brown band (band often disjunct on terga 5-8); abdominal sternum 9 pale (Fig. 2). Caudal filaments light brown.

Holotype: mature male nymph, Tonto Creek at Kohl's Ranch, Gila County, Arizona, 19 July 1970, R. K. Allen. **Paratopotypes:** 1 male and 1 female nymph, same data as holotype, in collection of California State College, Los Angeles.

Remarks: The only described species in the genus are known from South America. *Baetodes serratus* Needham and Murphy and *B. itatiyanus* Demoulin were described from Brazil, and *B. spiniferum* Traver is known only from Venezuela. *Baetodes sigillatus* would seem to be distinguished from the other described species by distribution alone as there are no records of North American species of mayflies occurring in South America. The nymphs of this species are further distinguished by possessing small dorsal median tubercles on abdominal segments 1-6 (Fig. 1), and by the presence of transverse reddish-brown bands on abdominal sterna 1-7 (Fig. 2).



Figures 1-2. The nymph of *Baetodes sigillatus*, new species: Fig. 1, abdominal terga, lateral view; Fig. 2, abdominal sterna, ventral view.

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AN INTRODUCED POPULATION OF SOCIAL WASPS, *POLISTES APACHUS*, THAT HAS PERSISTED FOR 10 YEARS (HYMENOPTERA: VESPIDAE)

The large social wasp *Polistes apachus* Saussure often builds its nests under the eaves of houses. This species has a typical life cycle for wasps of the genus. Overwintering queens, usually in groups of two to four, establish nests during April. Workers are produced until about midsummer, and then increasing numbers of sexual forms are produced. Observations made in this study indicate that nests terminate in September and October. When a nest terminates, reproduction ceases, the workers and males die, and the current season's queens eventually leave the comb. *Polistes apachus*, like all social wasps in North America, has an annual life cycle, and only the newly produced generation of queens survives the winter. There is some evidence that queens emerging from hibernation have a strong tendency to initiate nests in the area of the nest of the previous season. Using marked queens, Eberhard (Misc. Pub. Mus. Zool., Univ. Michigan, 140, 1969) found no movement of marked individuals of *P. fuscatus* (Fabricius) between neighboring buildings over a period of two years. This note reports the artificial establishment of a population of *P. apachus* that has persisted in the same general locality for 10 summers.

Ten nests of *P. apachus* were removed from the eaves of a house in Chatsworth, California during the middle of June, 1962. They were removed during the period when most nests have a few capped cells containing pupae, but very few adult workers. One nest appeared to have produced two workers, as two wasps were noticeably smaller than the others and two of the central cells were being reused. Each of the nests had at least one, and as many as five, wasps in attendance.

The wasp nests were transferred to wooden boxes. Each box was 14 × 18 × 30 cm, had a large plastic window and a hinged screen door, and was provided with a small petri dish of sucrose and water. Each nest was fixed to the roof of a box by a drop of polyvinyl chloride glue placed on the nest pedicel. The wasps were introduced into the boxes after the glue had dried.

A method similar to that described by Rabb and Lawson (J. Econ. Ent., 50:778-784, 1957) was used to relocate the wasp nests. The boxes were placed in the desired location and left there for three days. After this period, the screen door of each box was opened, allowing the wasps to resume normal foraging activities. In the present study, the new nest site was the roof of the science building of San Fernando Valley State College in Northridge, Cali-

fornia. This site was chosen because no *Polistes* nests of any species had been found in the overhangs of any of the buildings on campus because nests on the roof of the science building could not be disturbed. The nest boxes were fastened in a row to the top of a safety wall on the perimeter of the roofs. Each box was about 30 cm from any other box. The new nest site was 4 miles east and 1.3 miles south of the original location in Chatsworth.

After the 10 nests were relocated, they were observed through the summer and fall. All ten nests increased in size, produced sexual forms, and terminated in the fall. During the following spring (1963), *P. apachus* queens were observed flying about in the vicinity of the science building, and a number of new nests were started under an eave-like overhang immediately below the old nest boxes. This was the first time that nests of any *Polistes* species had been found on any building on campus.

Annual checks for active *P. apachus* nests on the science building and on two nearby buildings of similar structure were made each summer from 1962 to 1969. A final check, made in 1971, included the science building, the two nearby buildings, and four other similar buildings in the area. A tract of bungalows near the science building, included in the annual check until 1965, was also checked in 1971. Each year at least one nest was located in the immediate vicinity of the old nest boxes. More nests were found suspended from overhangs on other parts of the building, usually on the south side at the first floor level. For ten seasons, no *P. apachus* nests have been observed on the two nearby buildings. However, the bungalows, which had been free of *Polistes* nests in 1965, had a large *P. apachus* population in 1971.

This study confirms Eberhard's (1969) observations on the strong tendency of *Polistes* queens to start nests in the vicinity of the nest of the previous season. After ten seasons on the San Fernando Valley State campus, *P. apachus* is still restricted to the science building and to a nearby tract of bungalows. Consequently, some *Polistes* species are able to form populations that can persist for many generations in a very restricted locality, despite the annual termination of individual nests.

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THE PHYLLOSTOMATID BAT,
VAMPYRESSA BROCKI,
IN COLOMBIA

The species *Vampyressa brocki* was described from Guyana by Peterson (Life Sci. Contrib., Royal Ontario Mus., 73:1-17, 1968) on the basis of a single female. Subsequently, a male was obtained in Guyana (Peterson, Canadian Jour. Zool., 50:in press, 1972) and the species presently is known only from these two specimens. Between 28 June and 1 July 1969, while conducting studies on the karyotypes of phyllostomatid bats, we collected three additional specimens of this species in mature tropical rainforest at Leticia, Amazonas, Colombia. These bats were taken in mist nets at a height of no more than 3.5 meters over footpaths through the forest.

The measurements of our specimens (all adult females) TTU 8827, TTU 8832, and TTU 9047, respectively, as follows: Length of forearm, 35.4, 32.1, 33.2; length of hind foot, 8.5, 8.5, 9.5; length of ear, 11.0, 11.0, 11.5; greatest length of skull (including incisors), 18.4, 18.3, 18.4; condylobasal length, 16.0, 15.8, 16.2; zygomatic breadth, 10.9, 10.8, 10.7; breadth of braincase, 8.4, 8.4, 8.0; mastoid breadth, 9.4, 9.4, 9.5; interorbital constriction, 4.6, 4.6, 4.9; postorbital breadth, 4.9, 4.7, 5.1; breadth across molars (M1-M1), 7.9, 7.6, 7.8; breadth across canines (C-C), 4.2, 4.2, 4.3; length of maxillary tooth-row (C-M2), 5.7, 5.7, 5.7; palatal length (including incisors), 8.0, 8.2, 8.0; length of mandibles (condylo-incisive), 11.5, 11.5, 11.0; height of ramus, 3.7, 3.6, 3.7.

In all measurements, our females closely resemble those given for Guyanan specimens by Peterson (1968, 1972). However, in the key provided by Peterson (1968:13), bats with a forearm greater than 34 mm would be identified as *Vampyressa nymphaea*. One of our specimens has a forearm length of 35.4 but its greatest length of skull (18.4) identifies it as *V. brocki*, which is distinctly smaller than *V. nymphaea* in cranial dimensions.

In other characters, such as number of lower incisors, size and shape of lower premolars and m2, and absence of m3, our specimens are identical with those reported by Peterson. A dorsal stripe is present, but faint, in our specimens. The facial markings appear to be somewhat less distinct than those of the holotype as illustrated by Peterson (1968).

The karyotype of *V. brocki* is shown in figure 1. The diploid number is 24 and the fundamental number is 44. This karyotype is similar to that of *V. nymphaea* from Nicaragua and Honduras, which have a diploid number of 26 and a fundamental number of 48. *Vampyressa pusilla* from Leticia, Colombia, have a diploid number of 23 (males) or 24 (females), with a fundamental number of 24. Although the degree of chromosomal divergence be-



Figure 1. Representative karyotype of a female *Vampyressa brocki* from Leticia, Colombia.

tween *V. brocki* and *V. nymphaea* does not necessarily imply that the two taxa are specifically distinct, such divergence is typical of populations representing different species in the family Phyllostomatidae. Further, these chromosomal data suggest that *V. brocki* and *V. nymphaea* are more closely related to each other than either is to *V. pusilla*. These relationships were suggested by Peterson (1972).

Two females were pregnant when taken on 30 June and 1 July. The single embryo in each was minute. None of the three specimens evinced molt.

We thank C. J. Marinkelle of the Universidad de Los Andes for assistance during this study.

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TEMPERATURE CHANGES IN HEAT PRODUCING PLANTS

Heat production in aroid plant flowers was first noticed by Lamarck (Thomas, 1960) and at present the details of the biochemical and physiological mechanisms involved are well documented (Dormer, 1960; Fischer, 1960; Forward, 1960; Hackett, 1957; James and Beevers, 1950; James and Clapham, 1935; Meeuse, 1966). There are no records of the daily cycle of temperature within the spadix. Although a few temperatures have been recorded, there is no indication as to the magnitude of heat production, nor has there been much work reported on tropical aroids.

The cycle of temperature changes during flowering of *Philodendron selloum* on the campus of the University of California, Los Angeles, and in my own yard, Anaheim, California were recorded. All plants were in the shade for most or all of the day. Temperatures of 28 spadixes were taken with a Schult-

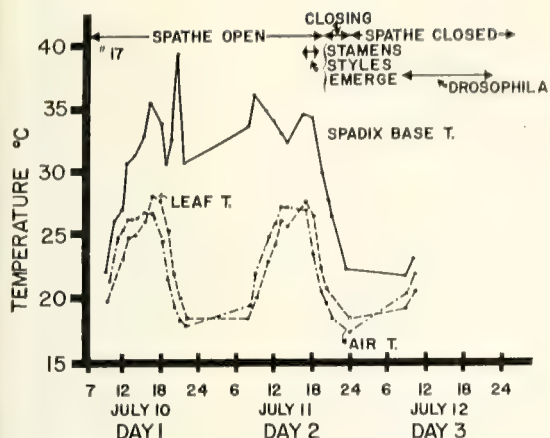


Figure 1. Spadix, leaf, and ambient temperatures of a single flower (17) of *Philodendron selloum*.

heis quick recording thermometer or with a YSI Telethermometer thermistor Model 44TD using vinyl 402 or banjo probes. Temperature readings were taken as follows: *spadix tip*, within center of spadix, 1" below tip; *spadix base*, within spadix 2" below beginning of female flowers; *air temperature*, within spathe but 1" away from and 2" above bottom of spadix; and *leaf*, 3" inside leaf base and 3" below spadix. Morning temperatures were taken between 0830–0930, afternoon: 1300–1700, night: 2000–2200 hrs.

The cycle for a typical flower is shown in figure 1. A summary of all temperatures is shown in figure 2. At no time was the ambient temperature, measured at spathe base, above 26.7°C. Air temperatures at night at UCLA were usually below 20°C with fog present, yet a maximum temperature of 42.5° (AT: 18.5°C) was recorded within the spadix base, a figure 24°C above ambient. Thus (Fig. 2) the spadix temperature is rising while the ambient is falling. The tip of the spadix begins to rise in temperature before the base, but the latter reaches a higher maximum temperature.

As noted by others (Dormer, 1960; James and Clapham, 1935) the emergence of the flowers from the solid spadix gives a shaggy appearance to the spadix. Flower emergence follows the night after maximum temperature is reached (night of day 2). This is followed by the beginning of a strong odor and the appearance of *Drosophila*. The flies crawl about the flower, presumably pollinating the flowers. The spathe subsequently closes accompanied by a drop in flower temperature, an increase in the odor, and the decomposition of the flower. The *Drosophila* are present within the closed spathe for several days after closing and presumably lay eggs in the decaying flower.

I wish to thank Allen Strickler, Beckman Instru-

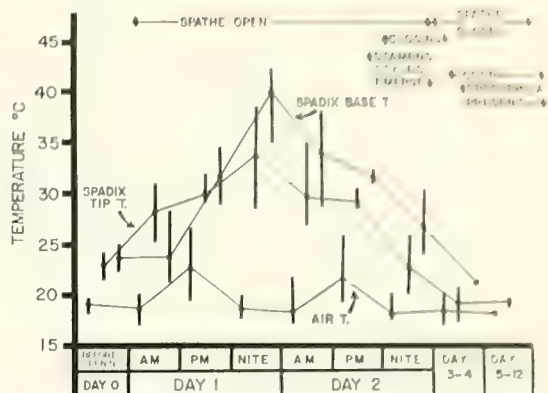


Figure 2. Summary of spadix and ambient temperatures of 28 *Philodendron selloum* flowering cycles. Vertical lines indicate range and dots indicate means.

ment Co., for calling my attention to this problem. Portions of this work were supported by the National Science Foundation (GB-2307, and a Senior Postdoctoral Fellowship, 56017).

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RANGE EXTENSIONS OF PORCELAIN AND HERMIT CRABS IN THE GULF OF CALIFORNIA

During 1970–1972 the senior author made numerous collections of intertidal invertebrates throughout the Gulf of California. From examination of these collections and one by Alex Kerstitch (University of Arizona) the following range extensions have been recorded.

Section Anomura Superfamily Galatheidea Family Porcellanidae

Petrolisthes edwardsii (Saussure)

Former northernmost records: Bahía de Santa Maria and Bahía de la Magdalena, west coast of Baja California, and Los Frailes, near the mouth of the Gulf of California (Haig, *Zoologica*, 53:57–74, 1968).

New record: Puerto Peñasco, Sonora, México, near the head of the Gulf of California; under stones in the mid-intertidal region; November 14, 1970; R. C. Brusca.

Petrolisthes sanfelipensis Glassell

Former southernmost record for west coast of mainland México: Guaymas, Sonora, México (Haig, Hopkins, and Scanland, *Trans. San Diego Soc. Nat. Hist.*, 16(2):13–32, 1970).

New record: Cabo San Lucas, Baja California Sur, México; November 28, 1968; Alex Kerstitch.

Petrolisthes hirtispinosus Lockington

Former northernmost record: Bahía de Tepoca, Sonora, México (Haig, *Allan Hancock Pac. Exp.* 24: 1–440, 1960).

New record: Puerto Peñasco, Sonora, México; under stones in the mid-intertidal region; November 14, 1970; R. C. Brusca.

Superfamily Paguridea Family Lithodidae Subfamily Hapalogastrinae

Hapalogaster cavicauda Stimpson

Former southernmost records: Punta Santo Tomas and San Geronimo Island on the west coast of Baja California (Garth, *Syst. Zool.*, 9(3):105–123, 1961).

New record: Guaymas, Sonora, México; under stones in the low-intertidal region; January 3, 1969; R. C. Brusca. We believe that this is the first record of the subfamily Hapalogastrinae from the Gulf of California.

RICHARD C. BRUSCA, *Dept. Biology, University of Arizona, Tucson, Arizona 85721* and JANET HAIG, *Curator of Crustacea, Allan Hancock Foundation, Los Angeles, California 90007.*

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INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and November) and includes articles in English in any field of science. Non-members will be assessed a page charge of \$40.00 per page. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current *AIBS Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, achieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous reference of pronouns, and logically placed modifiers.

MANUSCRIPT PREPARATION

It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit at least one additional copy with the original, on 8½ × 11 opaque, non-erasable paper, double spacing the entire manuscript. Do not break words at right-hand margin anywhere in the manuscript. Footnotes should be avoided. Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper must accompany a feature article.

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and literature cited. Avoid using more than two levels of subheadings.

A research note is usually one to six typewritten pages and rarely utilize subheadings. Consult a recent issue of the BULLETIN for the format of notes. Abstracts are not used for notes.

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Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International Code of Botanical Nomenclature (Lawjouw *et al.*, 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan *et al.*, 1958), and the International Code of Zoological Nomenclature (Stoll *et al.*, 1961). Special attention should be given to the description of new taxa, designation of holotype, etc.

The literature cited section should include six or more references; entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452-458.

Brattstrom, B. H. 1969. The condor in California. Pp. 369-382 in Vertebrates of California. (S. E.

Payne, ed.), Univ. California Press, xii + 635 pp.

If fewer than six references are cited they should be inserted in text as follows:

(McWilliams, Insect mimicry, p. 216, 1970); (Holmes and Speak, J. Mamm., 54: 452-458, 1971); (Brattstrom, The Condor in California, Pp. 369-382, in Vertebrates of California, 1969).

Tables and figures (line drawings, graphs, or black and white photographs) should not repeat data contained in the text. The author must provide numbers and short legends for tables and figures and place reference to each of them in the text. Legends should be typed on a separate sheet of paper and placed at the end of the manuscript. Illustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size; ordinarily they should be no more than twice the size of intended reduction and should not exceed 8½ by 11 inches in size. Photographs must be printed on glossy paper. Submit one photoduplicated copy of each illustration.

A cover illustration will be printed on the cover of each issue. This may be an illustration pertaining to an article in the issue or one of general scientific interest. Such illustrations along with a brief description should be sent to the technical editor for review.

PROCEDURE

All manuscripts should be submitted to the Technical Editor, Patrick H. Wells, Department of Biology, Occidental College, Los Angeles, California 90041. Evaluation of a paper submitted to the BULLETIN begins with a critical reading by the technical editor; several referees also check the paper for scientific content, originality, and clarity of presentation. Judgments as to the acceptability of the paper and suggestions for enhancing it are sent to the author at which time he may be requested to rework portions of the paper considering these recommendations. The paper is then re-submitted and may be re-evaluated before final acceptance after which it is sent to the managing editor.

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Photograph by William Morris, Occidental College.

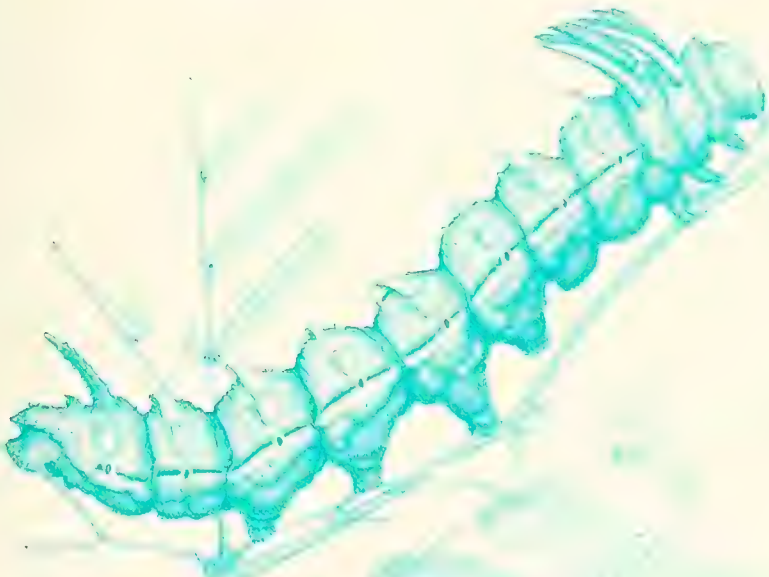
SOUTHERN CALIFORNIA ACADEMY OF SCIENCES

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Number 2



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BULLETIN OF THE SOUTHERN CALIFORNIA
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NUMBER 1

JOHN ADAMS COMSTOCK, 1883-1970

LLOYD M. MARTIN¹

At his home in Del Mar, California, the long and productive life of Dr. John Adams Comstock came to an end on December 26, 1970.

Born in Evanston, Illinois on January 30, 1883, he was a descendant of William Comstock, who arrived in Massachusetts, from England, in 1635. His father was John Adams, Sr., born October 2, 1845 in Franklin, Oakland Co., Michigan. His mother was Cornelia Hurd; daughter of Judge Harvey B. Hurd, one of the founders of Northwestern University. John Comstock married Caroline Townsend in 1905. They had three children: John Sterling, Jean, and Bette; all three now reside in California.

At an early age Dr. Comstock became interested in natural history, especially in entomology. Soon he narrowed his studies to the Lepidoptera. He was elected Secretary of the Chicago Entomological Society and served from 1898 to 1903. John was elected Recorder of the Entomological Section of the Chicago Academy of Sciences in 1903-1904. Because of his innate talent for illustration and design, he was given (1904) the position of Architectural Designer with Myron Hunt in Chicago. During the summers, he instructed in nature study at Vrilie Heights Summer School, Lake Geneva, Wisconsin.

In 1901, he and his brother Hurd travelled to Lake Josephine and Avon Park, Florida, to collect butterflies. Many fine specimens were obtained and some are still in the collection of the Natural History Museum of Los Angeles County. Later, in 1902, accompanied by Hurd, and a Professor Snyder, he went to Hall Valley, Colorado (in the Rocky Mountains). This party travelled all the way to Hayden where they caught many rare and little-known butterflies.

In the fall of 1905 he went to East Aurora, New York, to further his natural ability as a designer and writer. His furniture and book plate designing, book binding and illustrations, metal work, jewelry design, and associated creative work were

continued in the Roycroft Shop under the guidance of Elbert Hubbard. As a natural consequence of his love for the outdoors, he conducted nature study classes and brought nature-inspired designs into the Roycroft work.

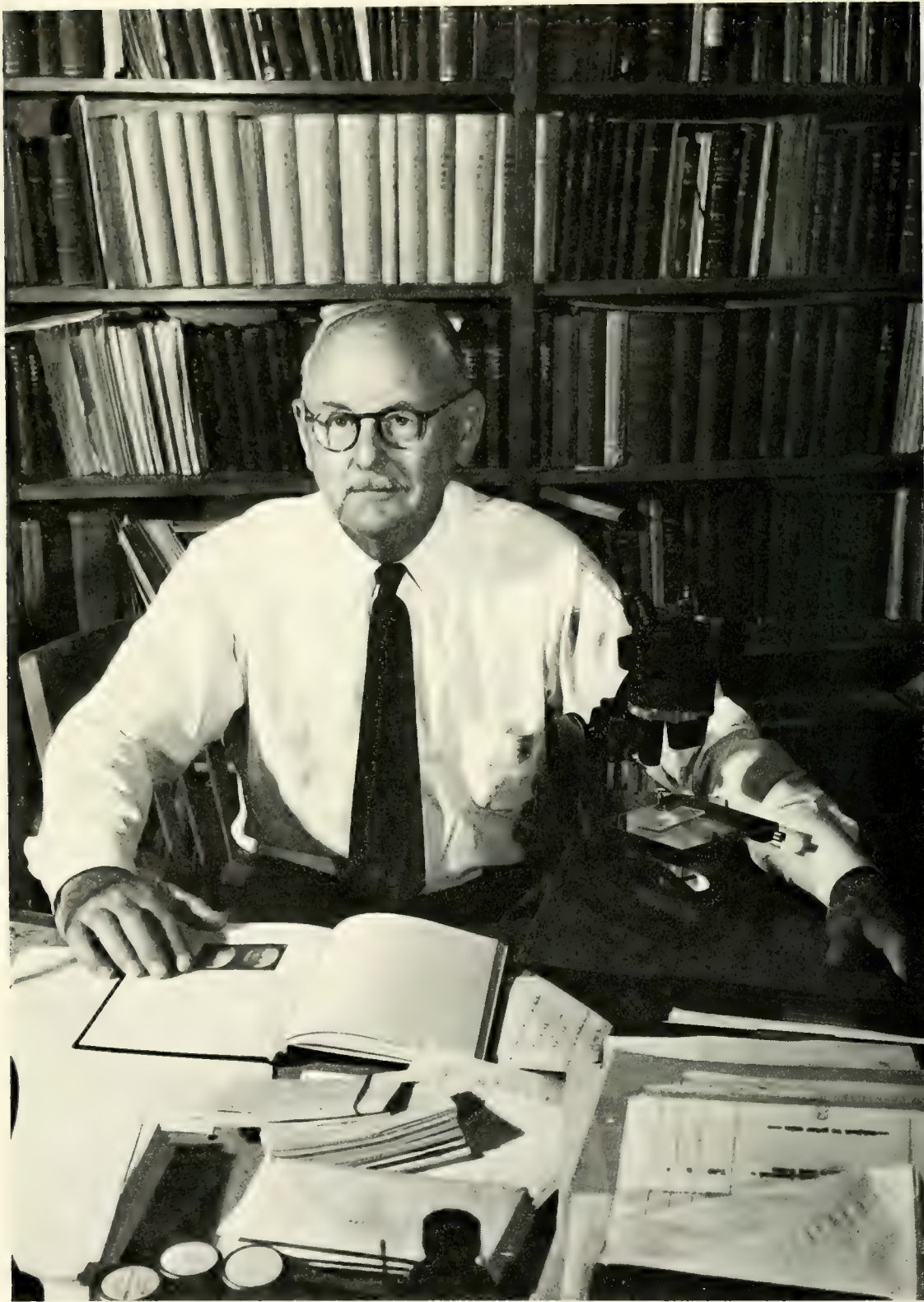
"The Doctor" moved with his family to Santa Rosa, California late in 1906. In 1908, he and his sister, Catherine Comstock Seideneck established the Craft-Camarata arts and crafts shop. He also worked for Luther Burbank, as a designer for Burbank's publications. In 1910, another Craft-Camarata was established in Santa Barbara, California.

Two years later John Comstock attended medical college in Los Angeles. During his summer vacations he taught the arts and crafts of jewelry and metal work at Carmel summer schools. In 1915, he was licensed to practice medicine and surgery in California and from 1928 to 1930 he was an honorary member of the attending staff of the Los Angeles County General Hospital.

During these years, his interest in entomology never wavered and he collected whenever time permitted. In 1917, he helped found and was elected the first president of the Lorquin Entomological Club (formerly a section of the Lorquin Natural History Club). The first meetings of the Club were held at the Los Angeles Public Library. In October of 1919, the club's meetings were held in the tower of the Southwest Museum. The club moved from the Southwest Museum in January, 1927 to the Natural History Museum of Los Angeles County where it became the Lorquin Entomological Society. These progressive changes were made possible by the constant work of Dr. Comstock.

The Royal Entomological Society of London elected Dr. Comstock as a Fellow in 1919. The same year he was appointed Assistant Director of

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JOHN ADAMS COMSTOCK

the Southwest Museum of Los Angeles and in 1921 was appointed Director of the Museum; a position which he held until 1926. At this time the fields of the Museum were restricted to anthropology, archeology, and history of the Southwest. The natural history exhibits and specimens of the Museum were turned over as an indefinite loan to the Natural History Museum of Los Angeles County. Dr. Comstock's entomological collections were transferred as a definite gift.

In 1922, while at the Southwest Museum, Dr. Comstock organized the Indian Welfare League and served as Executive Chairman, helping to secure beneficial legislation for Indians. In recognition of his efforts he was appointed to the Advisory Committee on Indian Affairs under Hubert Work, Secretary of the Interior. He served as Chairman of a Joint Parks Committee from 1925 to 1928 and worked to establish parks throughout the state of California.

John Comstock returned to private medical practice in 1926 at the Edwards-Wilbey Building in Los Angeles. His medical skills, along with his kindness, gentleness, and warmth toward his patients, made him an outstanding physician.

On March 28, 1928, he married Ruth Mary Gard, a descendant of an early California pioneer family. She now resides at their home in Del Mar, California.

The Doctor's interest in Lepidoptera took him, in 1924, to Moran, Wyoming, in the Jackson Hole region of the Teton Mountains; and to Mt. Washburn, in Yellowstone National Park. Many museums throughout the world have specimens from this extensive collecting trip. In addition to collecting specimens, he took many photographs on glass plates which he later tinted to bring out the natural beauties of the country.

Dr. Comstock became interested in the Southern California Academy of Sciences shortly after he arrived in Los Angeles. He was elected Secretary and editor of the *Bulletin* in 1921. He served as President of the Academy 1926-27. He continued as editor until 1962. In 1929 he was elected Fellow of the Academy. The financial assets of the Academy increased greatly under his guidance and the welfare and progress of this organization has benefited greatly from the many years of his close association.

An ambition to publish a book on the butterflies of California was realized on April 14, 1927. Dr. Comstock spent many years corresponding with outstanding lepidopteran collectors in California and in securing authentic records of Cali-

fornian species from various museums and private collections. *The Butterflies of California* still remains a classic and contains 63 color-plates which are exceptionally clear and precise.

Early in 1928 John Adam Comstock was appointed Acting Director of the Los Angeles County Museum of History, Science, and Art; on October 1, he was made Assistant Director. He was Director of Science from 1939 to 1942. At that time his title was changed to Chief Curator of the Science Division and after his retirement in November of 1948 he was given the position of Curator Emeritus of Entomology. After his retirement he remained closely associated with the Museum and on February 16, 1970 he was appointed Research Associate in Entomology for the fifth three-year period.

During his twenty years at the Natural History Museum John Comstock became a dearly loved member of the staff. His understanding of personal problems, his financial help, and his kind, gracious, and warm concern for his fellow man, helped many employees through the trying times of the "great depression" of the 1930's.

The Doctor's wide range of interests extended to genealogy and in 1930, he was elected President of the Los Angeles Genealogical Society. He was elected Life Fellow and given a Certificate of Merit by the Institute of American Genealogy in 1939. His book, *A History and genealogy of the Comstock family in America*, was published in 1949 and the enormous amount of information compiled in this book is extremely valuable.

During World War II, Dr. Comstock was active in the Station Wagon Evacuation Corps, Company D, First Evacuation Regiment of Los Angeles. As a medical doctor, his services were invaluable and greatly needed.

In addition to the above-mentioned societies, Dr. John Comstock was awarded many honorary memberships in Greek letter societies. These included Pi Gamma Mu (social sciences), Phi Sigma (biological sciences), and Sigma Xi (science).

After retiring from the Natural History Museum of Los Angeles County in 1948, John and his wife Ruth Comstock moved to Del Mar, California. He was unfailingly interested and active in civic affairs and in 1952, he served as President of the Del Mar Civic Association.

Dr. Comstock's continuing responsibility to preserving important California natural areas is exemplified by his efforts and those of his staunch conservation companion, Guy Fleming. Together

they fought to preserve the Torrey Pines in a natural state. The Doctor served as President of the Torrey Pines Association from 1955 to 1962.

His work at the San Diego Museum of Natural History was recognized with highest esteem. He was elected as President of the Fellows, San Diego Society of Natural History, for 1958 and served as a member of the Board of Directors of the San Diego Museum from 1957 to 1970 when he resigned due to age and poor health. His resignation was not accepted however, and instead the members of the Board voted him a Member Emeritus. He had been named Honorary Curator of Entomology for the San Diego Museum in 1969.

The Lepidopterists' Society elected him President in 1962 in recognition of the vast work that he had accomplished in working with young entomologists on the life cycles of butterflies and moths. In 1968, the Executive Council unanimously voted him an Honorary Life Member; an appointment which was confirmed by more than 80 percent of the membership.

During the period from 1932 to 1964 he made many trips to Arizona collecting large numbers of moths and butterflies, which he gave to the Natural History Museum of Los Angeles County. At the same time, he illustrated the early stages of many Lepidoptera that had not previously been described.

In November of 1952, Dr. Comstock accompanied by his wife Ruth, drove from the United States to the Guatemalan border. In the

spring of 1957 they went to Puerto Vallarta, Mexico, where they spent four months (June–October) collecting specimens. Much of the research from these expeditions to Latin America were published with Dr. Leonila Vasquez by Mexican foundation grants. Later he and his wife spent six months (May–October 1961) working in American Samoa where they resided in Mulinu in the country home of the former governor. The scientific knowledge accumulated in this area was published by the Bishop Museum of Hawaii.

His contributions to entomology, published in numerous scientific journals, number 220. He helped many entomologists who, through the years, have expressed great affection for him as an excellent worker in the field, and a delightful companion for fellow collectors. It would take many pages to record their reactions. His honors, positions, accomplishments, talents, personality, and affection for his fellow man will long be remembered by those who were fortunate to know him. His talents in art, science, medicine, and genealogy, and his qualities for leadership, have been widely recognized. In the words of Robert F. Heilbron, President of the Board of the San Diego Society of Natural History, "He was wise, gentle, always kind. His life touched ours and we were enriched. Now he is gone and we are diminished."

I wish to express my appreciation to Mrs. Ruth Comstock for information and her assistance in preparing this manuscript.

BIBLIOGRAPHY OF JOHN ADAMS COMSTOCK, 1883–1970

DEBORAH BIRNIE AND JAMES DALE SMITH¹

Between the years 1902 and 1969, Dr. John Adams Comstock, produced 236 scientific papers; the majority of which dealt with Lepidoptera of the southwest and Pacific coast. These papers include many excellent illustrations which attest to the Doctor's ability with pen and ink as well as water colors. In preparing Dr. Comstock's bibliography which follows, we have made several annotations, in brackets, in order to clarify the content of certain papers.

1902

A trip to Lake Josephine, Fla. [with Hurd Comstock].
Ent. News, 13(3):75–77.

An incident of Prof. Synder's trip in Colorado. Ent.
News, 13(8):258.

¹ Dept. Biology, California State University, Fullerton, California 92634.

1918

A new aberration. *The Lepidopterist*, 2(2):13, 1 pl.

Melitaea anicia: two new aberrations. *The Lepidopterist*, 2(5):34-37, 1 pl.

Notes on the *pola-minuta* group of *Melitaea*s, with description of a new species. *The Lepidopterist*, 2(7):55.

Notes on the *pola-minuta* group of *Melitaea*s, with description of a new species (cont.). *The Lepidopterist*, 2(9-10):70-73, 1 pl.

1920

A new species or race of *Argynnis* from California. *Southwest Sci. Bull.*, pp. 4-8, 1 pl.

Butterflies of California; Preliminary announcement. *Bull. So. California Acad. Sci.*, 19(3):4-8.

1921

Butterflies of California; the Swallowtails and allies. *Bull. So. California Acad. Sci.*, 20(1):5-6. [Plate 3 published BSCAS, 21(1):18].

Butterflies of California, (cont.) [The swallowtails and allies]. *Bull. So. California Acad. Sci.*, 20(2):45-46, 1 pl.

Studies in Pacific Coast Lepidoptera [Early stages of *Euphydryas sierra* Wright]. *Bull. So. California Acad. Sci.*, 20(2):46-47, 1 pl.

A giant Palm-boring beetle—*Dinapate wrightii*. *Bull. So. California Acad. Sci.*, 21(1):5-17.

Butterflies of California, (cont.) [Plate 3—Swallowtails and their allies]. *Bull. So. California Acad. Sci.*, 21(1):18. [Text for plate published earlier BSCAS, 20(1):5-6].

The Mission Indians of California. *The Golden West*, Nov. 1, p. 7, and Nov. 15, 4-5.

1922

Studies in Pacific Coast Lepidoptera, (cont.): Notes on the *acmon-neurona* group *Lycaenids*, with description of a new species. *Bull. So. California Acad. Sci.*, 21(2):43-48.

1923

Butterflies of California, (cont.): The Parnassians. *Bull. So. California Acad. Sci.*, 22(1):15-16, 1 pl.

Studies in Pacific Coast Lepidoptera [Early stages of *Melitaea neumogeni*]. *Bull. So. California Acad. Sci.*, 22(2):68-69.

Butterflies of California, (cont.) [The Parnassian]. *Bull. So. California Acad. Sci.*, 22(2):15-16, 1 pl.

1924

Butterfly migration. *The Ouzel*, 1(1):7-9.

Studies in Pacific Coast Lepidoptera: The red of a "lost species." *Bull. So. California Acad. Sci.*, 23(1):13-16, 1 pl.

Butterflies of California, (cont.): The Whites and allies. *Bull. So. California Acad. Sci.*, 23(1):18-20, 1 pl.

Studies in Pacific Coast Lepidoptera: New races of California butterflies. *Bull. So. California Acad. Sci.*, 23(2):51-52.

Butterflies of California, (cont.): The Whites and allies. *Bull. So. California Acad. Sci.*, 23(2):53.

Butterflies of California, (cont.): The Whites and allies. *Bull. So. California Acad. Sci.*, 23(4):124-125.

Butterflies of California, (cont.): The Whites and allies. *Bull. So. California Acad. Sci.*, 23(5):157.

A new record for California [*Papilio polydamas* in California]. *Bull. So. California Acad. Sci.*, 23(5):157.

Studies in Pacific Coast Lepidoptera, (cont.): A new *Melitaea* from Oregon. *Bull. So. California Acad. Sci.*, 23(6):173-174.

Studies in Pacific Coast Lepidoptera: Notes on the genus *Cercyonis*. *Bull. So. California Acad. Sci.*, 23(6):174-177. [Includes notes on the genera *Pieris* and *Eurymus*].

Butterflies of California, (cont.) [The Dwarf Yellows, Marbles, and Southern Marble]. *Bull. So. California Acad. Sci.*, 23(6):177-178, 1 pl.

Larva and pupa of *Desmocerus californicus* (Horn) [with Alonzo Davis]. *Bull. So. California Acad. Sci.*, 23(6):178-181.

1925

Studies in Pacific Coast Lepidoptera, (cont.): A new variety and two new aberrant forms of California butterflies. *Bull. So. California Acad. Sci.*, 24(1):3-4.

Butterflies of California, (cont.) [The Marble-Orange Tips]. *Bull. So. California Acad. Sci.*, 24(1):4, 1 pl.

Studies in Pacific Coast Lepidoptera: A new race of *Mitoura siva* Edw. in California. Bull. So. California Acad. Sci., 24(2):36-38.

Butterflies of California, (cont.) [The Marbles]. Bull. So. California Acad. Sci., 24(2):38, 1 pl.

Butterflies of California, (cont.) [The Sulphurs and Dog-faces]. Bull. So. California Acad. Sci., 24(3):61-62, 1 pl.

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1926

Butterflies of California, (cont.) [The Sulphurs]. Bull. So. California Acad. Sci., 25(1):28, 2 pls.

Studies in Pacific Coast Lepidoptera, (cont.): Thirteen new species or aberrations of California butterflies. Bull. So. California Acad. Sci., 25(1):29-34.

Studies in Pacific Coast Lepidoptera, (cont.): A new aberrant butterfly from southern California. Bull. So. California Acad. Sci., 25(2):48.

Butterflies of California, (cont.) [The Sulphurs]. Bull. So. California Acad. Sci., 25(2):62-65, 2 pls.

Butterflies of California, (cont.) [The Milkweed butterflies]. Bull. So. California Acad. Sci., 25(3):84-87, 1 pl.

1927

Butterflies of California. McBride Printing Co., (privately printed by John Adams Comstock), 1-334, 63 pls.

Protective coloration and mimicry. Bull. So. California Acad. Sci., 26(1):1-4.

1928

Studies in Pacific Coast Lepidoptera, (cont.) [Life history studies (eggs, larvae, and pupae) of six California Lepidoptera]. Bull. So. California Acad. Sci., 26(3):67-70.

Studies in Pacific Coast Lepidoptera, (cont.) [Life history studies of four California Lepidoptera]. Bull. So. California Acad. Sci., 27(2):63-67.

Studies in Pacific Coast Lepidoptera, (cont.): Early stages of *Calephelis australis* Edw. Bull. So. California Acad. Sci., 27(3):80-89.

1929

The egg of *Glaucompsyche lygdamus australis* Grinnell. Bull. So. California Acad. Sci., 28(1):6, pl. 5 on page 11.

Studies in Pacific Coast Lepidoptera, (cont.) [Life history studies of eight California Lepidoptera]. Bull. So. California Acad. Sci., 28(2):22-32.

A new species or form of *Anthocharis* from California. Bull. So. California Acad. Sci., 28(2):32-33.

1930

Studies in Pacific Coast Lepidoptera, (cont.) [Life history studies of eight California Lepidoptera]. Bull. So. California Acad. Sci., 28(3):50-58.

The life history of *Philotes sonorensis* Felder [with Carl Coolidge]. Bull. So. California Acad. Sci., 29(1):16-21.

Studies in Pacific Coast Lepidoptera, (cont.) [Life history studies of eight California Lepidoptera]. Bull. So. California Acad. Sci., 29(1):21-31.

1931

Studies in Pacific Coast Lepidoptera, (cont.) [Life history studies of four California Lepidoptera]. Bull. So. California Acad. Sci., 29(3):135-142.

Studies in Pacific Coast Lepidoptera, (cont.) [Life history studies of three California Lepidoptera]. Bull. So. California Acad. Sci., 30(1):15-20.

Notes on the life history of *Poanes melane* Edw. (Lepid.) [with Charles M. Dammers]. Bull. So. California Acad. Sci., 30(1):20-22.

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1932

The metamorphosis of *Heterochroa bredowii* californica Butl. (Lepid.) [with Charles M. Dammers]. Bull. So. California Acad. Sci., 30(3):83-87.

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Metamorphoses of six California Lepidoptera. Bull. So. California Acad. Sci., 31(3):88-99.

1933

A new lycaenid from Southern California [with Christopher Henne]. Bull. So. California Acad. Sci., 32(1):23-26.

Notes on the life histories of two California lepidopterous insects [with Charles M. Dammers]. Bull. So. California Acad. Sci., 32(1):27-37.

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THREE NEW SYMPATRIC *PLEOCOMA* FROM THE SOUTHERN SIERRA NEVADA MOUNTAINS OF CALIFORNIA (COLEOPTERA: SCARABAEIDAE)

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ABSTRACT: Two new species and one new subspecies of *Pleocomma* are described from sympatric populations in the Greenhorn Mountains of the southern Sierra Nevada range. Intraspecific character variation, comparison to closely related forms and biology are discussed following each description. An ecological description of the type locality is also presented.

Beetles of the genus *Pleocomma* have long been prized and much sought after by Pacific coast coleopterists, yet our knowledge of the habits and distribution of the genus is still rather fragmentary. The three new forms described herein help fill a large distributional gap between the central Sierra Nevada and Tehachapi Mountains. They also present the first recorded instance of three *Pleocomma* species occurring sympatrically. Refinements in collecting apparatus, easier access to remote areas, and increased knowledge of male *Pleocomma* flight habits will undoubtedly lead to the discovery of more such areas of species sympatry.

As in most populations of *Pleocomma* where series have been available for study, the three new taxa presented exhibit considerable minor morphological character variation. I have therefore selected as diagnostic characters those which appear most constant, both quantitatively and qualitatively.

Holotypes of new taxa described herein are on deposit in the Natural History Museum of Los Angeles County collection (LACM). Other institutions or persons receiving paratypes will be abbreviated in the text as follows: California Academy of Sciences, CAS; California Insect Survey, Berkeley, CIS; U. S. National Museum, USNM; F. T. Hovore, FTH; D. G. Marqua, DGM; C. E. Langston, CEL; T. W. Taylor, TWT; H. F. Howden, HFH; B. D. Streit, BDS; G. C. Walters, GCW; M. T. Gannon, MTG; R. L. Westcott, RLW.

Pleocomma marquai, new species

Figure 1

Description: *Male.* Form robust, oblong-oval, moderately convex, dorsum slightly flattened; integument mostly dark brown to piceous; pubescence reddish-golden. *Head* black, vertical horn and anterior process of clypeus thinly clothed with reddish-

golden hairs; dorsal surface closely, irregularly punctate, with broad smooth area extending from lateral base of vertical horn anteriorly to base of ocular canthus; clypeal process small, constricted at base, only moderately reflexed, anterior face slightly concave medially, apex with moderately deep, obtuse notch, apical angles of notch acute, rounded; vertical horn elongate, sides subparallel, apex with shallow, obtuse notch, apical angles of notch rounded, anterior face of horn evenly convex, surface coarsely punctate, punctures elongate, sparsely clothed with long reddish-golden hairs; ocular canthi projecting forward from a right angle, anterior edge sinuate, apex acutely rounded, dorsal surface concave, smooth except for few elongate punctures apically; palpi and antennae dark reddish-brown, scape and lamellae darker, scape stout, subconical, second segment moniliform, strongly flattened, third segment elongate, much shorter than scape, slightly reflexed, fourth segment cylindrical, slightly more than one-half as long as third segment, fifth segment strongly transverse with acute process, segments six to eleven distinctly lamellate, sixth segment with lamella about two-thirds as long as that of seventh segment, lamella of seventh segment slightly shorter than that of eighth segment, that of eighth distinctly shorter than that of ninth, lamellae of ninth and tenth segments subequal in length, that of eleventh only slightly shorter, ratios of segments six to eleven in holotype 20:30:32:36:36:35. *Pronotum* piceous, less than twice as wide as long (length-to-width ratio in holotype 5.85:10.8), widest at posterior angles, posterior angles broadly rounded, lateral discal impressions feeble, with indistinct reddish macula; disc evenly convex, anterior median impression lacking, pubescence entirely absent, surface shining, finely, moderately densely punctate, punctures denser anteriorly, less distinct and more widely spaced laterally. *Legs* dark reddish-brown to piceous, clothed with long reddish-golden hairs. *Scutellum* finely, sparsely punctate centrally, nearly glaucous. *Elytra* black, shining, finely, shallowly, irregularly punctate, sutural striae moderately impressed, dorsally

¹ Placerita Canyon Nature Study, Greenhorn Mountains, Placerita Canyon Road, Newhall, California 91325.

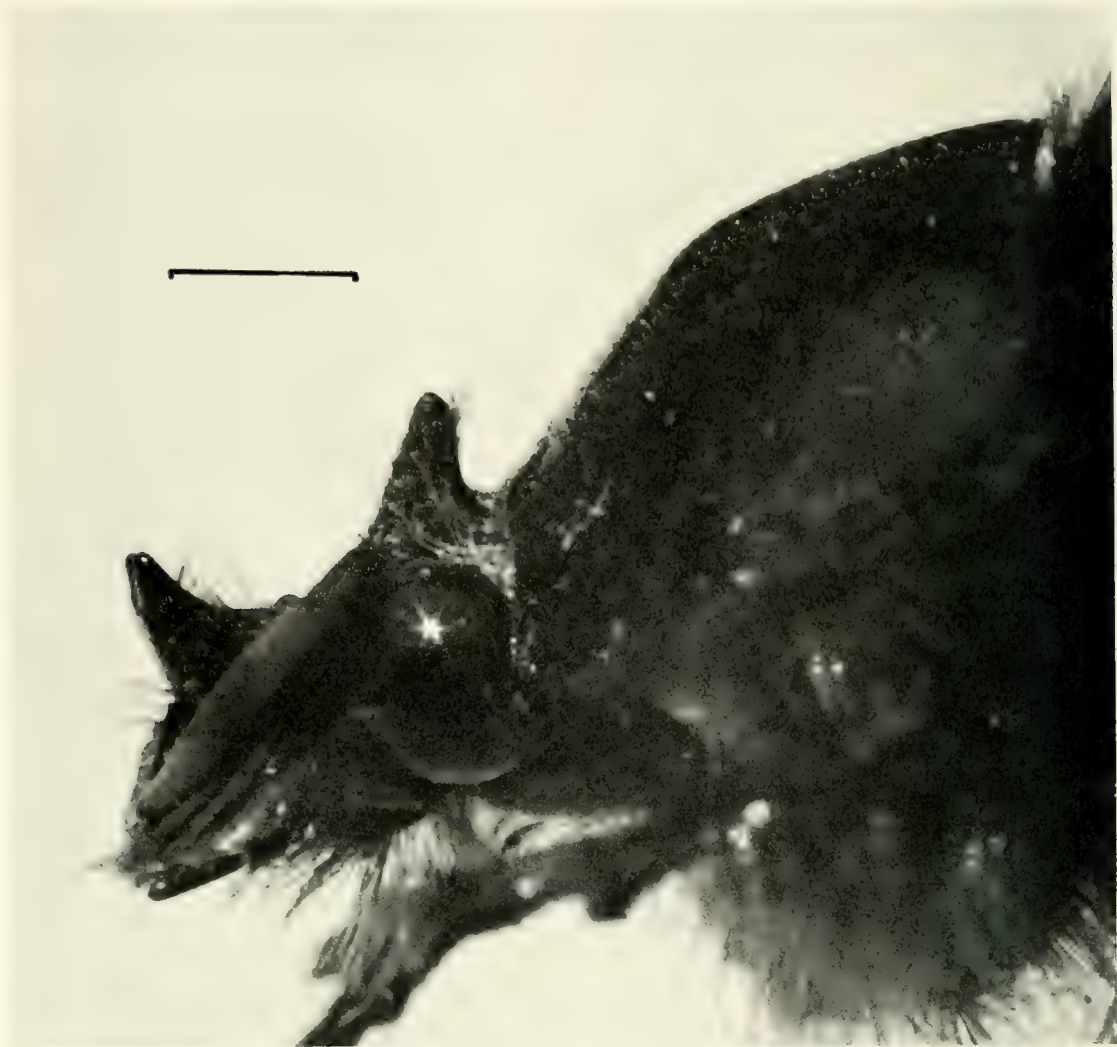


Figure 1. *Pleocoma marquai*, new species, left lateral view of head and pronotum, holotype (male). Scale equals 2 mm.

irregularly punctate, geminate striae at margins of costae feeble, indicated only by single row of fine, shallow punctures, costae with few minute punctures, not elevated. *Abdomen* dark reddish-brown, sternites moderately densely, irregularly punctate, punctures moderate in size, thinly clothed with reddish-golden pubescence. Length 22–28 mm.

Female. Form ovate, robust; color reddish-brown; pubescence pale reddish. *Head* with clypeus coarsely, densely punctate, expanded apically, apical angles acute, rounded, anterior margin feebly sinuate near median notch, median notch small, shallow, narrowly rounded; vertical horn very short, stout, apical notch broadly obtuse, rounded, apices rounded; antennae castaneous, lamellae slightly darker, third segment short, subcylindrical, about one and one-half times

longer than second segment, fourth segment slightly transverse, fifth segment with acute process, segments six to eleven distinctly lamellate, forming club, sixth segment with short lamella, lamellae of segments seven and eight subequal, only about three-fourths as long as that of segment nine, lamella of segment nine longest, those of segments ten and eleven slightly shorter than nine and of decreasing length. *Pronotum* convex, shining, dark reddish-brown, lighter laterally, less than twice as wide as long (length-to-width ratio in allotype 9:16.8), widest at posterior angles, posterior angles obtusely rounded, disc moderately, irregularly punctate, punctures larger and denser laterally and anteriorly, interrupted medially by vague longitudinal impunctate line. *Scutellum* finely, sparsely punctate anteriorly, few punctures with short re-

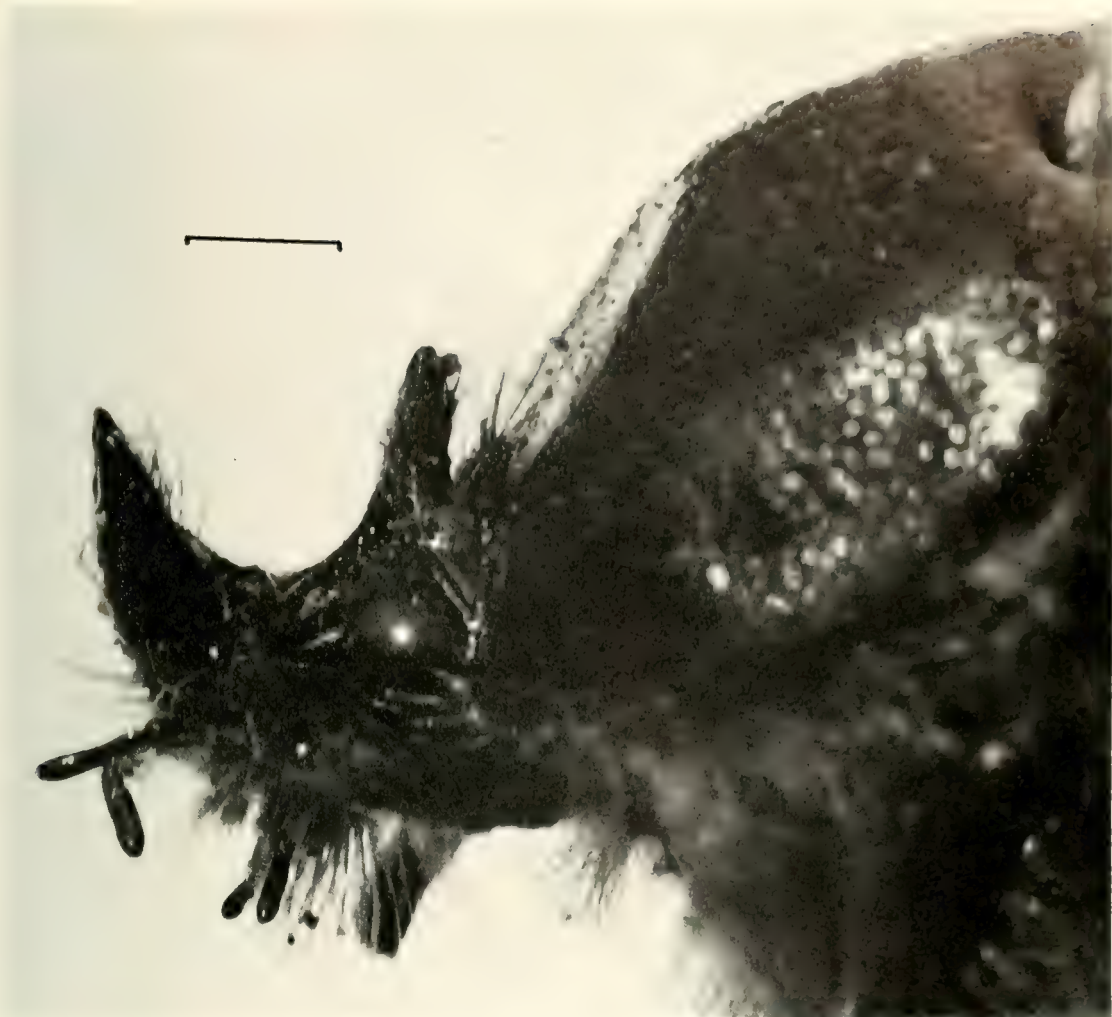


Figure 2. *Pleocoma fimbriata* Lec., left lateral view of head and pronotum, male. Scale equals 2 mm.

cumbent hairs. Elytra widest behind middle, transparent, surface shining, finely, irregularly punctate, costae elevated, nearly attaining elytral apices, sutural striae distinct, impressed, coarsely punctate, geminate striae at costae, feebly impressed, finely, irregularly punctate. Length 31–40 mm.

Holotype: Male, California, Tulare Co., Posey, 16 October 1971 (B. D. Streit) LACM. *Allotype*: Female, California, Tulare Co., Posey, 12 November 1971 (T. W. Taylor) LACM.

Paratypes (241): CALIFORNIA, Tulare Co., 144 ♂ 15 ♀, Posey, 8 November 1969 to 20 December 1969, 23 October 1970 to 26 October 1970, 15 October 1971 to 29 November 1971 (D. G. Marqua, T. W. Taylor, B. D. Streit, G. C. Walters, F. T. Hovore, C. E. Langston, Dawn, Rod, and Blaine Bryan, M. T. Gannon) DGM 17, TWT 31, BDS 42, FTH 12, CEL

7, GCW 21, LACM 4, USNM 3, HFH 4, RLW 4, CIS 5, CAS 4, MTG 5; 14 ♂ 5 ♀, .6 mi E Posey, 15 October 1971 to 25 October 1971 (F. T. Hovore) FTH; 23 ♂ 7 ♀, 1 mi N and 2 mi N Posey, 16 October 1971 to 1 December 1971 (C. E. Langston) CEL; 24 ♂, Balance Rock Resort, 16 October 1971 to 12 November 1971 (F. T. Hovore, B. D. Streit) FTH 4, BDS 20. Kern Co., 9 ♂, Glennville, 14 November 1968, 15 November 1969, 26 November 1970, 11, 12 November 1971 (D. G. Marqua, C. E. Langston, B. D. Streit) DGM 3, BDS 2, CEL 4.

Other specimens examined: CALIFORNIA, Tulare Co., 17 ♂, California Hot Springs, 13 October 1968, 6 November 1966 (David Fields, 4 with no collection listed).

Discussion and diagnosis. Both sexes of *P. marquai* can be immediately distinguished from

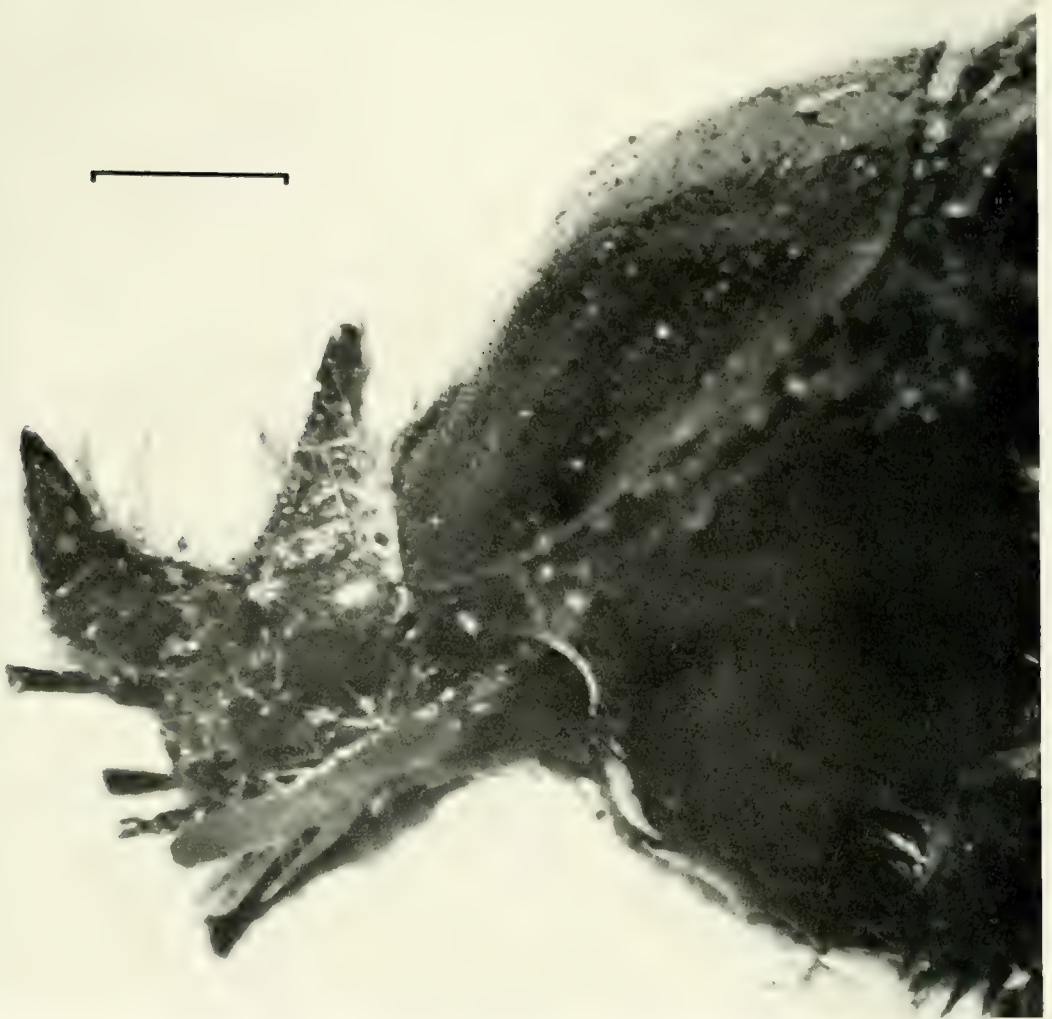


Figure 3. *Pleocoma tularensis* Leach, left lateral view of head and pronotum, paratype (male). Scale equals 2 mm.

their closest congeners, *P. fimbriata* Leconte and *P. tularensis* Leach, by the presence of distinct lamellae on antennal segments six and seven, with that of segment six two-thirds or more as long as that of segment seven. In both *tularensis* and *fimbriata*, segment six is at most angulate, segment seven sometimes with a short projection. Males of *P. marquai* may be further differentiated from *fimbriata* and *tularensis* by the fifth antennal segment which is strongly transverse with at least a short projection (at most slightly transverse in typical *fimbriata* and *tularensis*), and by the shorter, less strongly reflexed clypeal process (Figs. 1-3). In all specimens examined of *marquai* the pronotum is less than twice as wide

as long, while in the 59 males of *tularensis* examined, the pronotum is at least twice as wide as long in all but two specimens, or about 3 percent.

Pleocoma marquai represents the southernmost form of the *fimbriata-tularensis* species group. Thus far, the northernmost known locality for *marquai* is about 30 miles south of the southernmost recorded point of collection of *tularensis*, and it is highly probable that somewhere in the intervening area the two populations overlap.

Biology: Adults of both sexes and larvae of *P. marquai* have been collected from burrows beneath *Ceanothus cuneatus* Nutt., and it is probable that this plant serves as the primary larval host. *Pleocoma tularensis* males and females have



Figure 4. *Pleocoma rubiginosa*, new species, left lateral view of head and pronotum, holotype (male). Scale equals 2 mm.

been collected from pupal cells beneath *Ceanothus cuneatus* in Fresno County, and I have also collected female *P. fimbriata* beneath *Ceanothus* sp. (prob. *integerrimus* H. and A.) in El Dorado County. Although it appears that *Pleocoma* larvae are not necessarily oligophagous (Fellin, 1966), the fact that the three species in this group show an apparent preference for the genus *Ceanothus* as a primary host seems to substantiate their close biological relationship.

Adult activity of *P. marquai* in the vicinity of the type locality begins during or shortly after the

first precipitation of the fall season, usually in early October, and may continue until early December in years of relatively low rainfall. Males will fly throughout the night while it is raining or snowing, and at dusk for several days thereafter, during weather conditions varying from heavy overcast to bright late afternoon sunlight.

I take pleasure in naming this species after David G. Marqua, who first brought specimens of *Pleocoma* from the Posey-Glennville area to my attention, and who has made numerous contributions to this study.



Figure 5. *Pleocoma hoppingi* Fall, left lateral view of head and pronotum, male. Scale equals 2 mm.

***Pleocoma rubiginosa*, new species**

Figure 4

Description: Male. Form robust, broadly oblong-oval, moderately convex, dorsum slightly flattened; integument reddish-brown, pubescence pale reddish. *Head* dark reddish-brown, narrowly margined anteriorly with piceous, very densely clothed with long reddish hairs; dorsal surface irregularly, shallowly rugoso-punctate, with vague smooth area extending from anterior base of vertical horn laterally to apex of ocular canthus; clypeal process moderately reflexed, anterior face distinctly impressed medially, apex deeply, obtusely notched, apical angles produced, acute, rounded; vertical horn elongate, sides subparallel, apex with moderate rounded notch, apical angles acutely rounded, anterior face of horn only slightly concave medially, coarsely, irregularly punctate, punctures elliptical, surface clothed with

long reddish hairs; ocular canthi stout, subquadrate, projecting forward slightly from a right angle, anterior edge sinuate, dorsal surface slightly concave, nearly glabrous; oblique supra-orbital carina distinct, extending medially on ocular canthus; palpi and antennae light reddish-brown, lamellae of antennae slightly darker, scape stout, subconical, slightly flattened dorsally, second segment moniliform, strongly flattened, third segment elongate, subequal to scape in length, slightly angulated anterior at apex, fourth segment only slightly transverse, angulated, fifth segment strongly transverse with acute process, segments six to eleven distinctly lamellate, sixth segment with lamella about two-thirds as long as that of seventh segment, lamella of seventh segment more than four-fifths as long as that of eighth segment, that of eighth distinctly shorter than that of ninth, lamella of ninth segment longest, those of tenth and eleventh slightly shorter than ninth, and of decreasing length, ratios

of segments six to eleven in holotype 20:33:40:43:42:40. *Pronotum* less than twice as wide as long, barely widest at middle, sides broadly rounded, posterior angles broadly, obtusely rounded, lateral discal impressions feeble, maculate with piceous; disc convex, anterior median impression moderate, flattened, surface shining, densely, coarsely punctate except for narrow, median longitudinal impunctate line extending from anterior to posterior margins, entire surface of disc densely clothed with long, erect reddish hairs. *Scutellum* irregularly, moderately coarsely punctate, moderately densely clothed with long subrecumbent reddish hairs. *Elytra* rich reddish-brown, transparent, shining, fairly uniformly, finely, shallowly punctate, sutural striae moderately impressed, irregularly punctate, geminate striae at margins of costae feeble, indicated only by single row of fine, shallow punctures, costae impunctate, not elevated. *Abdomen* dark reddish-brown, sternites finely, moderately densely punctate, clothed with long reddish pubescence. Length 24–29 mm.

Holotype: Male, California, Tulare Co., 1 mi W Posey, 16 January 1972 (C. E. Langston) LACM.

Paratypes: 47 ♂, same locality as holotype, 2 January 1972 to 1 April 1972 (C. E. Langston) at blacklight trap, CEL 20, LACM 2, CAS 2, CIS 2, USNM 1, FTH 15, TWT 1, BDS 1, DGM 1, HFH 1, RLW 1.

Discussion and diagnosis: *Pleocoma rubiginosa* is perhaps only subspecifically related to *P. hoppingi* Fall, which it closely resembles in form and color. Males differ from *hoppingi* by the presence of only five long lamellae in the antennal club (seven in typical *hoppingi*), the absence of a flattened anteroventral process on the third antennal segment, the conspicuous median longitudinal impunctate line on the pronotal disc, the much more produced, more strongly reflexed clypeal process, and the longer vertical horn (Figs. 4–5). From the other similarly colored species, *badia* Fall and *linsleyi* Hovore, *rubiginosa* can be immediately distinguished by the fewer antennal lamellae (seven long lamellae in *badia* and *linsleyi*), densely hairy, heavily punctate pronotal disc, and subquadrate ocular canthi.

As in most of the other species of *Pleocoma*, males of *rubiginosa* exhibit some variation in external morphology. The relative lengths of the first few antennal lamellae vary slightly within the type series, but the basic diagnostic formula is sufficiently constant to distinguish *rubiginosa* from other closely related species. The absolute shape and size of the clypeal process is also somewhat variable, but in all specimens it is much more produced and more strongly reflexed than in any specimen examined of *hoppingi*.

Biology: Nothing is known of the larval habit of this species. The specimens of the type series were captured with blacklight traps from January to April, considerably later in the season than the normal major flight periods of other *Pleocoma* in the area. Although the traps were checked at various times during any given night, specimens were usually found in the traps in the morning indicating that males of *rubiginosa*, like those of several other species, fly most numerous at or slightly before dawn (Hazeltine, 1950, 1952; Hovore, 1971). Most of the specimens were collected during heavily overcast skies and fog, with light rain or snow. A few specimens were found in the traps during a week of warming weather following a major snowstorm, flight probably having been initiated by melting snow or ground ice. Late season flight habits have also been recorded for *P. hoppingi* on the South Fork of the Kaweah River (Fall, 1906); in the vicinity of Yosemite National Park (Linsley, 1941, 1942, 1943); and at Dry Meadow, Kern County (Linsley, 1957). It is probable that the last record refers to a population more closely related to *rubiginosa* than to typical *hoppingi*. Dry Meadow is in the Piute Mountains, about 24 miles south-east of Posey, while the type locality for *hoppingi* (South Fork of the Kaweah River, Tulare County) is approximately 48 miles north of Posey. Linsley (1938b) lists *hoppingi* from Kernville, approximately 8 miles east of Posey, and this record undoubtedly refers to a specimen of *rubiginosa* rather than typical *hoppingi*.

Pleocoma hirticollis reflexa, new subspecies

Figure 6

Description: *Male*. Form robust, oblong-oval, convex, dorsum only slightly flattened; integument reddish-brown to piceous; pubescence pale golden. *Head* black, vertical horn and anterior process of clypeus moderately densely clothed with long, pale golden hairs; dorsal surface irregularly punctate; clypeal process pronounced, strongly reflexed, nearly parallel with vertical horn, anterior face deeply concave medially, apex with deep, acutely rounded notch, apical angles acute, rounded; vertical horn elongate, sides subparallel, apex with shallow, obtusely rounded notch, anterior face of horn evenly convex, surface coarsely punctate, punctures elongate; ocular canthi nearly right angular to longitudinal midline of head, anterior edge sinuate, apex broadly, acutely rounded; dorsal surface concave, irregularly punctate; posterior antennae dark reddish-brown, scape and lamellae much slightly darker, scape stout, subconical, second seg-



Figure 6. *Pleocoma hirticollis reflexa*, new subspecies, left lateral view of head and pronotum, holotype (male). Scale equals 2 mm.

ment moniliform, flattened, third segment elongate, subcylindrical, slightly reflexed, fourth segment strongly transverse with short projection, segments five to eleven distinctly lamellate, fifth segment with lamella more than four-fifths as long as lamella of sixth segment, lamella of sixth segment only slightly shorter than lamella of seventh segment, lamella of seventh segment subequal to that of eighth segment, that of eighth segment slightly shorter than that of ninth segment, ninth longest, lamellae of tenth and eleventh segments subequal, slightly shorter than that of ninth. *Pronotum* piceous, more than twice as wide as long, widest at posterior angles, posterior angles rounded, lateral discal impressions distinct, maculate with pale reddish-brown; disc strongly convex, irregularly clothed with long, suberect pale hairs, anterior median impression indicated by narrow flattening of anterior surface, surface shining, densely, irregularly punctate, punctures small to moderate in

size on disc, larger anteriorly. *Scutellum* finely, moderately densely punctate, moderately clothed with long recumbent hairs. *Elytra* rich chestnut-brown, transparent, shining, finely, shallowly, irregularly punctate, sutural striae moderately impressed, irregularly punctate, geminate striae at margins of costae feeble, indicated only by single row of fine, shallow punctures, costae impunctate, not elevated. *Abdomen* reddish-brown, sparsely punctate, thinly clothed with long, pale golden hairs. Length 20–25 mm.

Female. Form robust, convex; color reddish-brown, pubescence pale golden. *Head* with dorsal surface densely, coarsely rugoso-punctate; clypeus expanded apically, apical angles obtuse, anterior margin bisinuate, median notch small, very shallow, rounded; vertical horn very short, stout, apical notch shallow, rounded, anterior face deeply impressed medially; ocular canthi subtriangular, anterior edge feebly



Figure 7. *Pleocoma hirticollis vandykei* Linsley, left lateral view of head and pronotum, male. Scale equals 2 mm.

sinuate, apices acutely rounded; antennae reddish-brown, scape and lamellae slightly darker, third segment elongate, subequal to scape in length, fourth segment with acute projection, about one-third as long as lamella of fifth segment, segments five to eleven lamellate, forming club. *Pronotum* dark reddish-brown, lighter laterally; slightly less than twice as wide as long, widest at posterior angles, posterior angles obtuse, rounded; disc convex, shining, surface coarsely rugoso-punctate, punctures forming indistinct transverse rows, denser and larger anteriorly, lateral discal impression feeble, maculate with piceous. *Scutellum* sparsely punctate medially, few punctures with short erect hairs. *Elytra* pale reddish-brown, transparent, surface shining, finely, irregularly punctate, sutural striae feebly impressed, indicated by single row of punctures, geminate striae at margins of costae indistinct, finely, shallowly punctate, costae only slightly elevated, nearly attaining elytral apices. Length 29–31 mm.

Holotype: Male, California, Tulare Co., 1 mi N Posey, 18 December 1971 (C. E. Langston) at blacklight trap, LACM. *Allotype*: Female, Tulare Co., 1 mi W Posey, 3500 ft, 27 February 1972 (F. T. Hovore) dug from pupal cell, FTH.

Paratypes (17): CALIFORNIA, Tulare Co., 12 mi N, 1 mi N Posey, 18 December 1971, 21 December 1971 (C. E. Langston) at blacklight trap, CEL 5, FTH 3, CAS 1, CIS 1, LACM 1, USNM 1. Kern Co., 2 mi N, Glennville and vicinity, 14 January 1970, 18 January 1970 (D. G. Marqua), DGM; 1♂, Glennville, 26 November 1970 (F. T. Hovore) FTH; 1♂ Glennville, 26 November 1970 (C. E. Langston) TWT, 1♂ Glennville, 25 November 1970 (Dawn Bryan) TWT.

Discussion and diagnosis: Three apparently distinct forms of *Pleocoma hirticollis* Schaufuss can be recognized: *P. hirticollis vandykei* Linsley (Fig. 7) occurs in the grassland regions surrounding San Francisco Bay; the nominate subspecies *P. h. hirticollis* Schaufuss, has been reported to

the Sierra Nevada foothills of Yuba and Nevada Counties; *P. h. reflexa* occurs in the foothills of the Greenhorn Mountains along the Kern-Tulare County border. Males of the three subspecies may be distinguished as follows:

Third segment of antenna usually angulate anteriorly, lamella of fourth segment one-third or more as long as that of fifth segment, lamella of eighth segment usually longest; clypeal process moderate, slightly reflexed; elytra chestnut-brown. Length 25–28 mm. Yuba and Nevada Counties, California *hirticollis* Schaufuss (1870).

Third segment of antenna usually not angulate anteriorly, lamella of fourth segment less than one-third as long as that of fifth segment, lamella of ninth segment usually longest; clypeal process reduced, only feebly reflexed; elytra piceous to black. Length 17–24 mm. Alameda, Sonoma, and Yolo Counties, California
..... *vandykei* Linsley (1938).

Third segment of antenna usually not angulate anteriorly, fourth segment of antenna transversely angulate or with vestigial lamella, much less than one-third as long as that of fifth segment, lamella of ninth segment usually longest; clypeal process very pronounced, strongly reflexed; elytra chestnut-brown. Length 20–25 mm. Kern and Tulare Counties, California *reflexa* Hovore.

In the type series the specific diagnostic characters are remarkably constant. The anterior clypeal process exhibits slight variation in size and in the depth of the median notch, but in all specimens the clypeus is more pronounced and much more strongly reflexed than in any specimen seen of either *vandykei* or *hirticollis*. The color of the pronotum in the male may vary from reddish-brown to piceous.

Biology: Males of *reflexa* in the vicinity of the type locality have been collected only after the area has received several inches of precipitation, with dates ranging from late November to mid-January. Most specimens were collected at night or at dawn, during or shortly after a drizzling rain. I collected a male at incandescent light shortly after dusk following a day of clear cold weather, and it is probable that male activity continues for several days subsequent to a major flight.

The allotypic female and two larvae were dug from their burrows in a grassy clearing, at depths

of from one to four inches. The paratype female was found in a schoolyard baseball field. It is possible that the larvae of *reflexa* feed upon grass rootlets, as do those *vandykei* (Smith and Potts, 1945; Ritcher, 1947), but the soil from which they were dug is interlaced with numerous rootlets of *Ceanothus cuneatus* and *Quercus Douglasii* H. and A., and a definite feeding preference has not yet been observed.

ECOLOGY OF THE TYPE LOCALITY

The sympatric occurrence of three distinctly different species of *Pleocoma* is unique in the recorded distribution of the genus. There are several localities known where two species are sympatric, and three species (*fimbriata*, *hirticollis*, and *edwardsi* Leconte) have been recorded from the vicinity of Nevada City, Nevada County, California. However, the exact localities of their collection have not been documented in sufficient detail to establish a definite area of sympatry.

The site near Posey where *P. rubiginosa*, *P. marquai*, and *P. h. reflexa* are sympatric is in a rather poorly defined ecotonal area. The grassy hillsides surrounding the site are dotted with deciduous Blue Oaks (*Quercus Douglasii* H. and A.) and Buckbrush (*Ceanothus cuneatus* Nutt.), characteristic of the Foothill Woodland plant community, while the shaded canyon bottoms hold mature stands of Yellow Pine (*Pinus ponderosa* Dougl.), Incense Cedar (*Libocedrus decurrens* Torr.), Alder (*Alnus* sp.), Maple (*Acer macrophyllum* Pursh.), and Willow (*Salix* sp.). Yellow Pine and Incense Cedar indicate the lowest influence in this area of the Yellow Pine Forest plant community (Munz and Keck, 1970), which predominates at higher elevations.

The blacklight traps from which the specimens were collected were placed near private dwellings along the bottom of a well-drained west-facing canyon at an elevation of approximately 3500 ft. The north-facing canyon side is dominated by large Black Oaks (*Quercus Kelloggii* Newb.), with brush cover primarily composed of low-growing stands of Gooseberry (*Ribes* sp.), Blackberry (*Rubus* sp.), Rose (*Rosa californica* Cham. and Schlect.), Buckbrush, and Mountain Mahogany (*Cercocarpus betuloides* Nutt.). A thick carpet of leaves covers much of the slope, and the soil beneath is a poorly consolidated clay loam. On the drier, south-facing canyon sides the dominant tree is the Blue Oak, with brush cover widely spaced, composed of Buckbrush, Coffeeberry

(*Rhamnus californica* Esch.), Elderberry (*Sambucus mexicana* Presl.), Mountain Mahogany and Honeysuckle (*Lonicera interrupta* Benth.). The groundcover consists of numerous grasses and small annuals, with Mariposa Lilies (*Calochortus* sp.) and Buckwheat (*Eriogonum* sp.) abundant in May and June. The soil varies from hard-packed decomposing granite to a loose clay loam.

Pleocoma marquai shows no evident preference for a particular soil type, and is extremely abundant beneath most stands of Buckbrush. The elevation range observed for *marquai* is from approximately 2900 ft to 4500 ft, and roughly follows the irregular lower margins of the Woodland-Forest ecotonal area. The vegetation mix is similar to that of the recorded localities for *fimbriata* and *tularensis*. These areas usually receive snow only during the colder winter storms, often not until late in the season. The flight periods of *marquai*, *tularensis*, and *fimbriata* are somewhat earlier than those of most other *Pleocoma* species in the Sierras, and in normal winters they will have experienced their major period of adult activity before the first significant snowfall.

Pleocoma rubiginosa has only been collected at the type locality, at an elevation of 3500 ft, although its affinities are to species which favor higher elevations. Its closest congener, *hoppingi*, has been recorded from 4000 ft to above 6000 ft, and specimens of an undescribed species in the "*hoppingi* group" have recently been collected on the eastern side of the Sierras at elevations up to 10,000 ft. It is therefore probable that *rubiginosa* is more widely distributed in the Yellow Pine Forest community above the Posey site, and probably does not occur much lower than 3400 ft.

The affinities of *P. h. reflexa* are to *Pleocoma* populations primarily found in foothill grassland areas, and at the Posey site specimens have been dug from the soil on the south-facing slope in an open grassy clearing. The other localities for *reflexa* are also in the grassy Foothill Woodland community, at 3150 ft and 3700 ft elevations. It is probable that *reflexa* is the most widely distributed *Pleocoma* in this area, as it would appear to have the widest potential area of suitable habitat. If the larva is in fact a mobile rootlet feeder in grassy areas, *reflexa* could conceivably occur in several floral communities at elevations both higher and lower than presently recorded. The *hirticollis* species group is found in both the Coastal and Sierra Nevada Ranges, and may ultimately prove to be the most widespread and evenly distributed species in the genus.

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A REVIEW OF *EUCYLLUS* HORN (COLEOPTERA: CURCULIONIDAE, BRACHYRHININAE, PERITELINI)

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ABSTRACT: The genus *Eucyllus* Horn is reviewed with the three species: *vagans* Horn, *unicolor* Van Dyke, and *echinus* Van Dyke, redescribed and discussed. Three additional species are described as new: *saesariatus* from Sonora, Mexico, and Arizona, *carinarostris* from California, and *cinereus* from California. *Eucyllus tinkhami* Tanner is placed in the genus *Eucilinus* Buchanan. Distributional and biological information is given for each.

While we were reviewing the Peritelini it became evident to us that the whole tribe was in need of study. Many new species were encountered in fieldwork in western North America. Because an abundance of material exists and several new species required description, the genus, *Eucyllus* Horn was chosen as a starting point.

The following standard abbreviations (Arnett, *et al.*, 1969) are used: BYUC—Entomological collections, Brigham Young University; CASC—Entomological collections, California Academy of Sciences; CIAN—Centro de Investigaciones Agrícolas del Noroeste; CSCLB—Entomological collections, California State University, Long Beach; ELS—E. L. Sleeper collector; ELSC—E. L. Sleeper collection; FWPC—Frank W. Pelsue collection; INIA—Instituto Nacional de Investigaciones; LACM—Natural History Museum of Los Angeles County; and USNM—United States National Museum.

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EUCYLLUS HORN

Eucyllus Horn, 1876:74.

Encyllus Van Dyke, 1936:31, (*lapsus*).

Type species: *Eucyllus vagans* Horn, by monotypy.

Description: Rostrum slightly longer than broad, continuous with head; epistoma smooth, divested of scales, triangular in shape with carinate margins, and a fringe of 10–12 setae bordering the carinate margins; head not as long as broad, with smaller and more abundant punctures than rostrum, little or no sculpturing; antennae inserted in the basal third of rostrum; scrobe a flat-bottomed channel with no pronounced convex area distad of the eye. Funiculus with seven segments, vestiture of scales and setae similar to remainder of body; scape feebly arcuate attaining anterior margin of prothorax; club oval-acuminate, clothed with short fine setae. Eyes nearly round,

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Figures 1–10a. Spermathecae of *Eucyllus*. 1. *Eucyllus vagans* Horn, Mexico, Baja California Norte, Puertecitos, V-31-58. 2. *E. vagans*, California, San Bernardino Co., Upper Lucerne Valley, X-2-64. 3. *E. vagans*, California, San Diego Co., Pamitas Spring (3 mi W Carrizo Springs, III-1-58. 4. *E. vagans*, Mexico, Baja California Norte, Laguna Salada, II-20-59. 5. *E. saesariatus*, new species, Mexico, Sonora, 51 mi E San Luis, XII-30-60, paratype. 6. *E. carinarostris*, new species, California, Riverside Co., Pinto Wash Well, II-17-62, holotype. 7. *E. unicolor* Van Dyke, Nevada, Nye Co., 19 mi SE Lathrop Wells, III-24-70. 8. *E. echinus* Van Dyke, Nevada, Lincoln Co., 10 mi N Hwy. #91 on Elgin Road, V-18-62. 9. *E. echinus*, Mexico, Sonora, 51 mi E San Luis, XII-30-60. 10. *E. cinereus*, new species, California, Inyo Co., Grandview P.C., VIII-10-65, paratype. 10a. *E. cinereus*, a different individual. Line represents $\frac{1}{2}$ mm.

strongly convex, and coarsely faceted. Prothorax not as long as broad, sides feebly arcuate, anterior margin truncate, posterior margin rounded. Scutellum small, obscured by elytra. Elytra nearly twice as long as broad; humeri rounded, feebly prominent, sides parallel, tapering to apex; striae defined by round deep punctures, setae usually arranged in two longitudinal rows alternately spaced on the interval. Venter of body with vestiture similar to dorsum; however, the recurved setae are slender, and truncate at apices; pro- and mesocoxae contiguous with metacoxae, widely separated. Femora one-third longer than tibiae, beginning rather slender and gradually becoming clubbed distally, no teeth or definite spines present, vestiture of scales and recurved setae similar to other parts of the body; tibiae slender, broadening distally, vestiture similar to femora, apex with teeth, tibiae 1 and 2 with a short mucro, tibia 3 without mucro; tarsus with first segment as long as second and third combined, fourth segment almost as long as first three segments combined, dorsal vestiture of segments 1-3 recurved setae and scales, fourth segment with fine setae.

Remarks: Horn described *Eucyllus* in 1876 placing it between *Dysticheus* Horn and *Thinoxenus* Horn, a placement retained by all subsequent workers through Kissinger (1964). *Eucyllus* Horn, *Thinoxenus* Horn, *Dysticheus* Horn, *Rhypodillus* Cockerell, *Eucillinus* Buchanan, and two undescribed genera form a group of morphologically very similar genera. The described genera can be separated easily in Kissinger (1964).

Eucyllus, for the most part, inhabits arid habitats of the desert (Fig. 32). With the exception of *E. cinereus*, members of this genus are restricted mostly to the Creosote Bush Scrub plant community, with *E. echinus* and *saesariatus* barely reaching into the Mesquite-Grassland plant community. *Eucyllus cinereus* is found in Pinyon-Juniper communities. The other genera of the group are coastal or montane.

Eucyllus remained monotypic until 1936 when Van Dyke added two species; *E. echinus* and *unicolor*. In this paper we are describing three new species of *Eucyllus*, bringing the total number of species to six.

In 1959, Tanner described *Eucyllus tinkhami*. Upon re-examination of paratypes of this species, particularly the proventriculus and tibial apices, we conclude that it does not belong in *Eucyllus* and is in fact a subspecies of *Eucillinus* (*Thysanochorhinus*) *aridus* Van Dyke. It should then be known as *Eucillinus* (*Thysanochorhinus*) *aridus tinkhami* (Tanner), new combination. The type locality for *E. aridus aridus* is Cronise Lake, Cali-

fornia, approximately 35 miles northwest of the Kelso Dunes; the type locality of *E. aridus tinkhami*.

The paucity of specimens of *Eucyllus* in collections results from the fact that members of the genus are nocturnal and seek refuge about the bases of food plants during the daylight hours when most insect collectors are active. *Eucyllus vagans* and *saesariatus* have been taken at night throughout the year.

Species of *Eucyllus* are largely parthenogenetic; males being less frequently encountered than females. Populations from south and east of the Colorado River have a higher frequency of males than those encountered elsewhere. In the material available to us, *E. echinus* from Arizona has a male-female ratio of 1:2.5; whereas, in *saesariatus* it is 1:1.25. Males were not found in the population of *E. echinus* from Nevada and Utah, *E. unicolor*, or *E. carinarostris*.

Eucyllus vagans has an interesting change in sex ratio from south to north in its range. In Baja California del Norte, Mexico (the extreme southern part of the range) the male-female ratio approaches 1:1 from below sea level to about 1000 ft elevation. No males are known from above 1000 ft. In the vicinity of Borrego Valley and the Salton Sea in California the ratio is 1:1.5. From north of the Riverside-Imperial County line or the vicinity of the northern end of the Salton Sea, only one male is known. It is a very old specimen, presented to Sleeper by J. G. Shanafelt who verified that the data were correct. It bears the locality label "Taquitiz Cyn. nr. Palm Sprs." From the remainder of the range northward and northeastward for more than 260 miles, no males are known.

In all species, except *cinereus*, the number of mature ova per female at the time of peak production varied from 5-10, with a mean of 8.25 per female. There seemed to be no significant difference between species as to ova number. Ova averaged 0.5 mm in *echinus* and 0.65 mm in *vagans*. *Eucyllus vagans* deposits approximately 250 eggs over a one to two month period after which ova production nearly ceases. Ova are deposited in the soil about the bases of the food plant.

In the four species in which males are known, there are three distinct types of aedeagi. In the larger species the aedeagi are very long, slender and twisted at the apical third, terminating apically in a more slender, elongate, blunt knob (Fig. 20). In *echinus* the aedeagus is rather short, parallel-

sided and tapering apically to an abrupt, blunt apex, not curved or twisted (Fig. 21). The aedeagus of *cinereus* is short, narrowed, and blunt at the apex (Fig. 19).

The spermathecae are useful for separating the species. Both fresh and dried specimens were dissected; no detectable differences were noted between either.

KEY TO THE SPECIES OF *EUCYLLUS*

1. Larger species, 4.5–7.7 mm in length; second segment of funiculus almost twice as long as third 2
- 1'. Smaller species, 3.7–5.3 mm in length; second funicular segment slightly longer than third ... 3
2. Setae of dorsal surface of body 4–7 times as long as broad, a few only 2–3 times as long as broad, acute to blunt apices, with a strongly arcuate concavity on posterior side; feeble indication of a median sulcus on rostrum (Fig. 28) *vagans* Horn
- 2'. Setae of dorsal surface of body 10–15 times as long as broad with a few 4–7 times as long as broad, acute apices, with feebly arcuate concavity on posterior side; rostrum with a feeble indication of a median carina (Fig. 31) *saesariatus*, new species
3. Setae of dorsal surface as much as three times as long as broad, blunt at apices, erect and appearing club-like 4
- 3'. Setae of dorsal surface not more than twice as long as broad, recurved and peg-like in appearance 5
4. A rather robust species with many dark patches on the elytra and prothorax, overall color straw; setae robust and erect; feeble indication of a median carina on dorsum of rostrum posterior to the epistoma (Fig. 23); spermatheca as in figures 8–9 *echinus* Van Dyke
- 4'. A smaller species, uniformly gray in color with a few darker patches; setae finer than preceding species, prominently erect; spermatheca as in figures 10–10a *cinereus*, new species.
[Note: the recently described species *Eucyllus horridus* Hatch (1971:265) will key to *cinereus*. It appears that *horridus* is not a *Eucyllus*, but belongs to an as yet undescribed genus of Peritelini. Although this casts some doubt on the placement of *cinereus* in *Eucyllus*, it seems wise to leave all species in their present status until the new genera of this group are described.]
5. Strong median carina posterior to epistoma (Fig. 22); spermatheca as in figure 6 *carinarostris*, new species
- 5'. Feeble indication of a median sulcus posterior

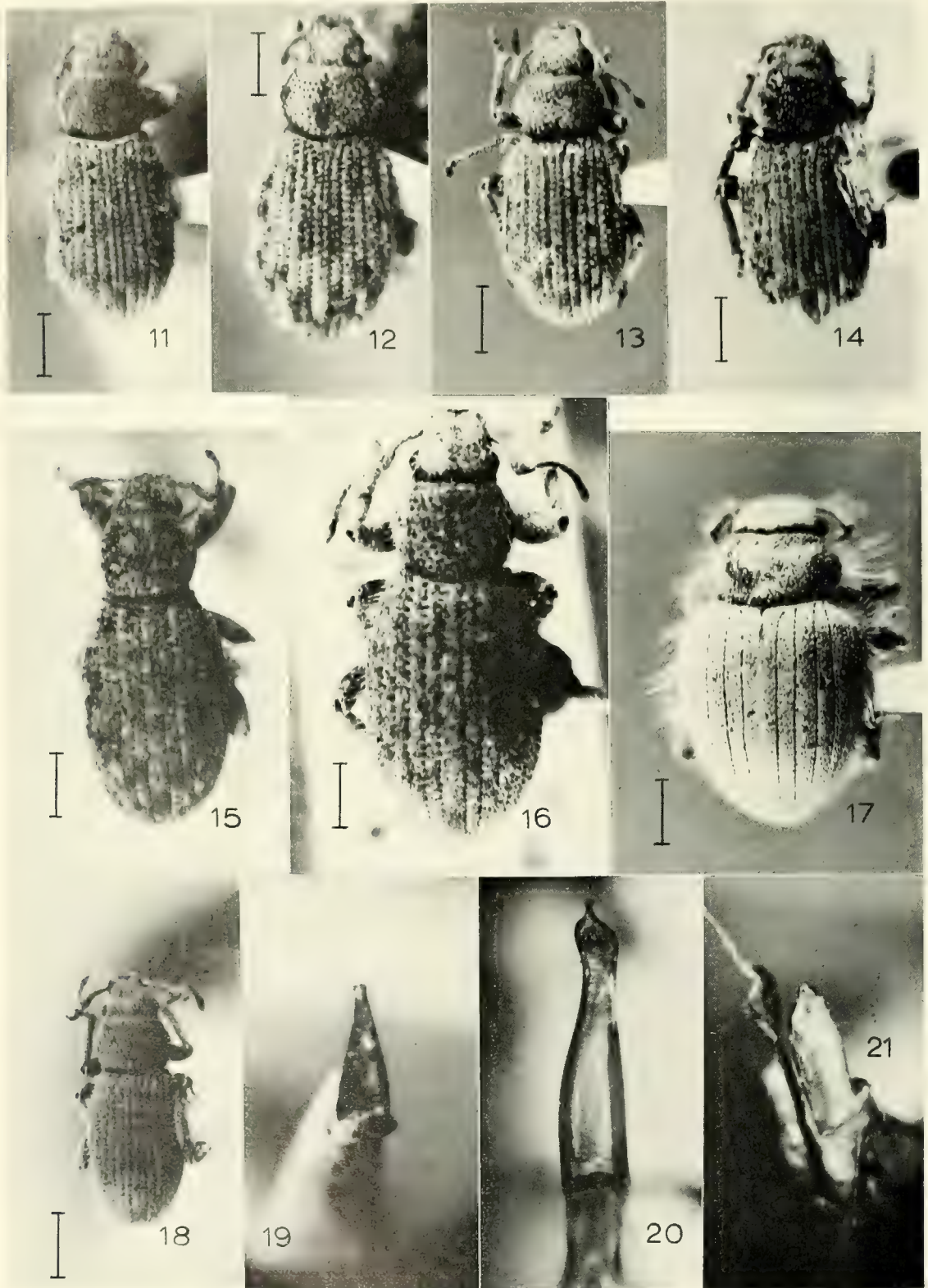
to epistoma; spermatheca as in figure 8 *unicolor* Van Dyke

Eucyllus vagans Horn Figures 1–4, 15, 28, 30

Eucyllus vagans Horn 1876:76 Type locality—"Arizona and California adjacent." Here restricted to Carrizo Springs, Imperial Co., California. The only specimen in the Museum of Comparative Zoology, Harvard University was examined and is designated lectotype. It bears the following data: 1) gold disc (= California), 2) 1937, 3) Type, 4) *Eucyllus vagans* Horn, 5) Lectotype label-(A female).

Description: Body length 4.5–7.7 mm (mean 5.85; ♀ 6.77 mm); width 2.3–3.5 mm (mean ♂ 2.56; ♀ 3.03 mm); elongate oval; vestiture brownish gray with silver patches on the head, prothorax and abdomen. Body densely clothed with white and silver triangular scales; moderately clothed with erect to suberect and recurved seta-like scales, set in deep punctures, four to seven times longer than broad at base with acute to nearly blunt apices. Shape of elongate setae, in cross section, indicates a strongly arcuate concavity. Rostrum clothed with white scales with a small silver patch dorsad of each eye and a median patch extending from posterior margin of the head to just past the anterior margin of the eyes; strongly sculptured with large punctures, this evident when denuded; with feeble indication of dorsal sulcus extending from just posterior of epistoma almost to head. Head feebly sculptured with smaller and more abundant punctures than rostrum. Funiculus with first and second segment same length, second twice length of third. Prothorax with vestiture of white scales with three longitudinal stripes of brown to silver scales; disc coarsely punctured with nearly round deep punctures with a mean of 17.1 per .25 mm² and rather uniform in distribution. Elytra with dirty white scales and several irregular patches of silvery to brown scales forming no definite pattern. Femora with band of silvery scales at distal third; apical comb of tibia with anterior teeth rather short and thick, becoming slightly longer and thinner towards posterior. Aedeagus long and rather slender, sides almost parallel for basal third of length tapering for another third then broadening again twisting down, tapering to a blunt knobbed apex; spermatheca as in figures 1–4.

Distribution: California, Inyo Co., 8.5 mi SW Westgard Pass, 6000 ft. eastward (below 6000 ft) to Nevada, Nye Co., Cane Springs, thence to the Mormon Mountains in Lincoln Co., Washington Co., Utah, southeastward to near Colorado City, Arizona, westward to Littlefield, Arizona, south to the Colorado River, west of the Colorado to the delta in Baja California del Norte then south to Mission





Figures 22–31. 22. Rostrum of *Eucyllus carinarostris*, ♀, California, Riverside Co., Pinto Wash Well, III-17-62, holotype. 23. Same of *E. echinus*, ♀, Mexico, Sonora, 51 mi E San Luis, XII-30-60. 24. Same of *E. unicolor*, ♀, Utah, St. George. 25. Apical setae of *E. echinus*. 26. Same of *E. cinereus*. 27. Same of *E. unicolor*. 28. Rostrum of *E. vagans*. 29. Apical setae of elytra of *E. saesariatus*. 30. Same of *E. vagans*. 31. Rostrum of *E. saesariatus*. Figures of various scales.

Figures 11–21. 11. *Eucyllus unicolor*, ♀, St. George, Utah. 12. *E. echinus*, ♀, Arizona, Pinal Co., Picacho, V-1-42. 13. *E. echinus*, ♀, Mexico, Sonora, 51 mi E San Luis, XII-30-60. 14. *E. carinarostris*, ♀, California, Riverside Co., Pinto Wash Well, II-17-62, paratype. 15. *E. vagans*, ♀, California, San Diego Co., 3 mi W Carrizo Springs, XI-15-58. 16. *E. saesariatus*, ♀, Mexico, Sonora, 51 mi E San Luis, XII-30-60, holotype. 17. *Eucyllus* (*Thysanotus*) *aridus tinkhami*, ♀, California, San Bernardino Co., Kelso Dunes, V-25-58, ELS. 18. *E. cinereus*, ♀, California, Inyo Co., White Mts., Grandview Public Camp, VIII-10-65, ELS. 19. *E. cinereus* aedeagus. 20. *E. saesariatus* aedeagus. 21. *E. echinus* aedeagus. The line equal to 1 mm. Figures 19–21 no scale.

TABLE 1. Size of *Eucyllus vagans* Horn from south to north. All measurements in millimeters. Each sample contained 30 randomly selected individuals.

Length		Width	
Mean (range) $\pm$ SD		Mean (range) $\pm$ SD	
<i>Mission Calamujue, 900 ft., Baja California del Norte</i>			
♂	5.45 (4.5–5.8) $\pm$.012		2.38 (2.0–2.6) $\pm$.013
♀	6.23 (5.5–6.9) $\pm$.014		2.78 (2.5–3.1) $\pm$.026
<i>Vicinity of Carrizo Springs, 250 ft., Imperial Co., California</i>			
♂	5.90 (5.3–6.4) $\pm$.011		2.51 (2.4–2.6) $\pm$.0006
♀	6.31 (5.5–6.8) $\pm$.012		2.76 (2.4–3.0) $\pm$.002
<i>Indian Cove, Joshua Tree National Monument, Riverside Co., California*</i>			
♀	6.17 (5.0–6.5) $\pm$.012		2.77 (2.2–3.0) $\pm$.025
<i>Lucerne Valley, 3000 ft., San Bernardino Co., California*</i>			
♀	6.66 (6.2–7.7) $\pm$.013		3.01 (2.8–3.6) $\pm$.003
<i>Wildrose Ranger Station, Panamint Mts., 4200 ft., Inyo Co., California*</i>			
♀	5.19 (4.5–5.7) $\pm$.012		2.39 (2.1–2.6) $\pm$.020
<i>Lathrop Wells, 2900 ft., Nye Co., Nevada*</i>			
♀	6.12 (5.5–6.7) $\pm$.014		2.74 (2.5–3.1) $\pm$.002

* No males found in sample.

Calamujue, northwest to El Rosario, eastward around the south end of the Sierra San Pedro Martir, thence north along the eastern slopes of this mountain range (below 2000 ft) over San Matias Pass, south to La Parra on the northwestern slope of the Sierra San Pedro Martir, north to Valle de la Trinidad to San Matias Pass northward along the eastern flanks of the Sierra de Juarez into California, throughout the Colorado Desert parts of Southern California to Banning and Morongo Valley, around and along the north flank of the San Bernardino and San Gabriel Mountains north to Mojave and throughout the Owens Valley wherever *Larrea* occurs (Fig. 32). A total of 4286 specimens were examined.

Remarks: *Eucyllus vagans* is the most plastic member of the genus and may represent a complex of species. Morphological variation presented several problems in this respect. Isolated pockets of this species appeared, superficially, to be distinct. Certain of these populations (for example, those from Valle de la Trinidad, Baja California del Norte, and Wildrose Ranger Station in the Panamint Mountains, Inyo County, California) are so different in scalation as to be easily distinguished from the remainder of the specimens examined. These could be separable as subspecies.

However, the authors do not feel it wise to name subspecies in parthenogenetic species. No significant differences were found in the spermathecae, although body proportions varied in the different populations. Table 1 indicates the range in lengths and widths and their respective means.

As can be seen from the means in table 1, specimens from Wildrose Ranger Station are relatively smaller and broader than the other samples. The means of leg lengths, antennal proportions, and other body proportions follow a similar pattern. The sample from Valle de la Trinidad was not large enough to analyze (only 15 specimens).

In *vagans* there is a relationship between setal length and age. Newly emerged specimens have rather elongate pointed setae (not approaching length of *saesariatus*). The tips of these setae break or wear off shortly after emergence in most individuals resulting in the broader, blunter scales normally considered typical of *vagans*.

The selection of Carrizo Spring as a type locality was based on two factors. First, other species of snout beetles collected and described at about the same time have this as a type locality (= Carisa Creek). These species have been recently collected with *E. vagans* at this location. This location was a stage and rest stop where the travelling collectors, of that time, would have felt safe to wander around collecting specimens. Second, material taken there seemingly represents the typical species (as currently recognized) and this population has a sex ratio of males to females of about 1:1.

Biology: *Eucyllus vagans* has been encountered under or feeding upon a larger variety of plant species than any of the other species. These include *Larrea tridentata*, *Franseria dumosa*, *Hymenoclea salsola*, *H. monogyra*, and *Atriplex* spp. The species also has been taken in pitfall traps and walking over blacklite and white light sheets.

Newly emerged forms appear on vegetation in May or June depending upon the latitude. The newly emerged individuals feed briefly, then most become dormant until October. Occasional stragglers are taken year around on the host plants, particularly *Hymenoclea* and *Larrea*.

Eucyllus saesariatus, new species

Figures 5, 16, 20, 29, 31

Holotype: Female, Mexico, Sonora, 51 mi E San Luis, XII-30-60, ELS, in ELSC #80. **Allotype:** Male, same data as holotype. Length 6.3 mm; width 2.7 mm.

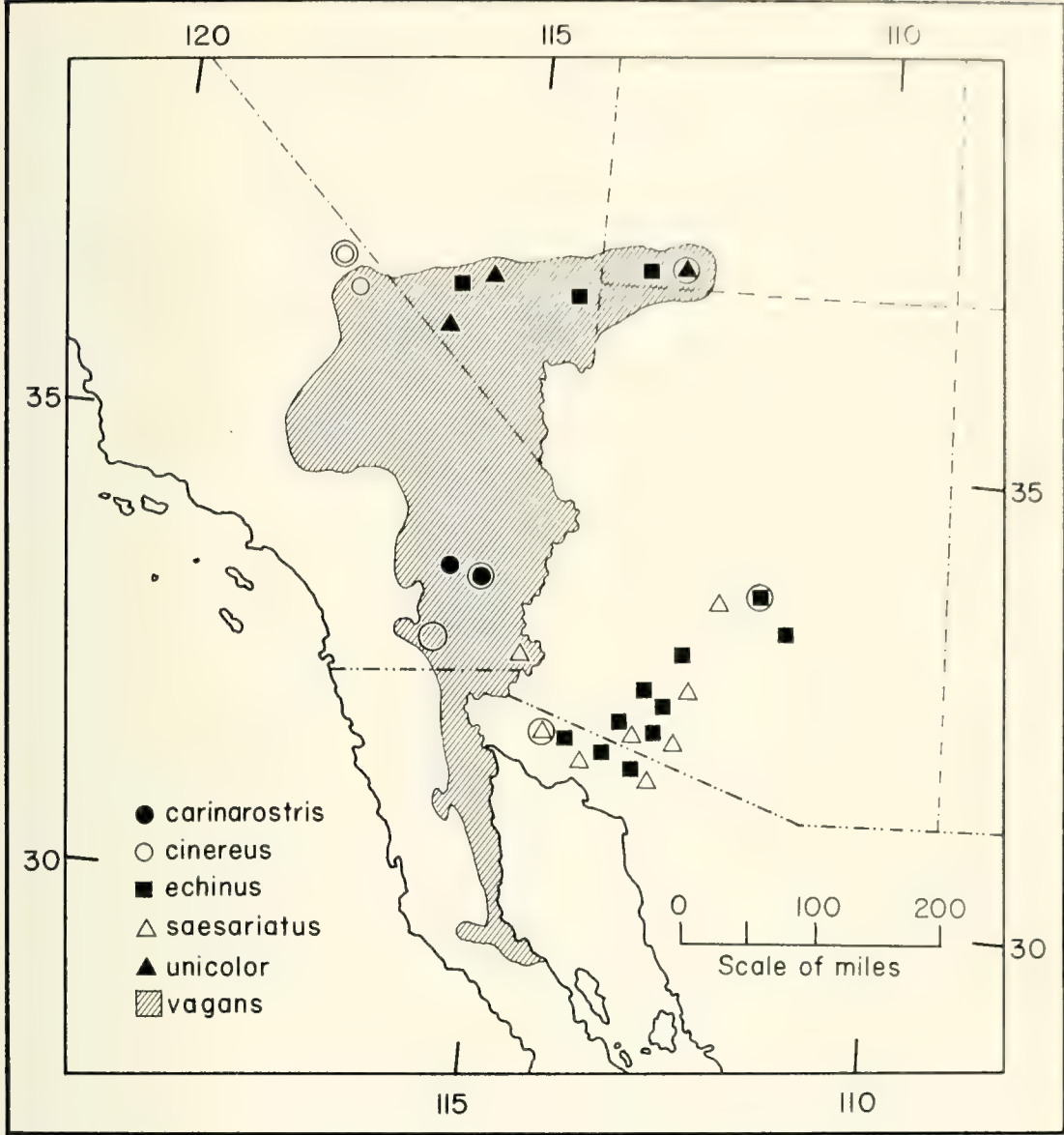


Figure 32. Distribution of *Eucyllus* species in the United States and Mexico. Symbol enclosed in a circle indicates the type locality for the species.

Differing little from the holotype, except for concavity in sternites 1 and 2. Aedeagus similar to *vagans* (Fig. 20).
Description: Length 7.1 mm; width 3.4 mm; elongate oval; vestiture dirty gray with silver to brownish patches on the head, prothorax, and abdomen; seta-like scales erect, ten to fifteen times longer than broad with some four to seven times as long as broad, all setae with acute apices; in cross section, setae with a feebly arcuate concavity. Rostrum slightly longer than broad; posterior to apex of

epistoma a feeble indication of a median carina with a teardrop-shaped fovea on each side of the carina forming a "V", distad to the carina a deep oval pit, this evident only when denuded; rostrum strongly sculptured when denuded. Funiculus with first segment as long as second, second segment almost twice as long as third. Prothorax dirty white with three longitudinal stripes of silver scales; disc with four irregular punctures with a mean of 13.5 per 25 mm. Elytra dirty white, with irregular patches of brown scales. Femora with a band of brown scales.

near distal end; apical comb with short thick teeth anteriorly gradually becoming longer and thinner toward posterior margin. Spermatheca as shown in figure 5.

Paratypes: 2♂, 10♀ same data as holotype, 9♂, 20♀ 52 mi E San Luis, XII-27-60, 10♂, 20♀, IX-30-68, ELS. Size of paratypes: length, 5.6–8.0 mm (mean ♂ 6.45; ♀ 7.13 mm); width 2.5–3.6 mm (mean ♂ 2.84; ♀ 3.31 mm). Paratypes deposited in the following collections: CASC, CIAN, CSLB, CWOB, ELSC, FWPC, INIA, LACM, and USNM.

Other specimens examined: MEXICO. *Sonora*, 72 mi E San Luis, VIII-22-60 (T. Schowalter); 57.9 mi W Sonoyta, IV-14-62; Sa. Pinacate, 2 mi S Mexico #2, I-26-62. CALIFORNIA. Imperial Co., Imperial Dam, V-3-58. ARIZONA. *Pima Co.*, (the following locations in Organ Pipe Cactus National Monument) Alamo Wash ½ mi E Hwy. #85, II-23-62, V-26-62; Bonito Well, II-12-61; Dos Lomitas XII-29-60; 15.8 mi N Headquarters, X-29-62; Quitobaquito, XII-28-60, X-28-61, I-24-62, VIII-5-62; Ajo Mtns., X-16-35, Bryant, CASC. *Maricopa Co.*, Picacho, V-1-42 and VI-28-41, Bryant, CASC. ?UTAH. *Washington Co.*, St. George, Wickham, CASC, (probably a labeling error). A total of 432 specimens examined. Unless noted otherwise, material was collected by ELS and is in ELSC.

Remarks: This species is very similar to *E. vagans*; however, it can easily be differentiated by the length of the seta-like scales on the dorsum, morphology of the spermatheca, and the feeble indication of a median carina on the rostrum. Greater morphological continuity of specimens from different locations (Fig. 32) is seen in this species than in *vagans*. This may be due to the existence of males in all the locations recorded.

Biology: All of the material was collected from *Larrea tridentata* at night. The adults feeding on vegetation are most numerous in late December and early January. A few stragglers are present year around.

Eucyllus echinus Van Dyke

Figures 8, 9, 12, 13, 21, 23, 25

Eucyllus echinus Van Dyke 1936, 31. Type locality—"Cave Creek, Maricopa Co., Arizona." (CASC 4144 Ent.) a female. Holotype examined.

Description: Body length 4.0–5.3 mm (mean 4.9); width 1.8–2.2 mm (mean 2.1); elongate oval; vestiture brown to dirty gray; derm black, with irregular patches of brownish silver scales; seta-like scales twice as long as broad, truncate at apices or slightly rounded, appearing club-like and erect. Rostrum having a feeble indication of a median carina extending from epistoma to posterior margin of head; strongly sculp-

tured when denuded. Funiculus with first, second, and third segments nearly same length, slightly longer than scape. Head feebly sculptured with a few rather small, oval punctures, which are most evident when denuded. Prothorax with irregular dark patches; disc with large deep punctures with a mean of 24.3 per .25 mm². Elytral vestiture brownish in color with irregular dark patches. Femora uniformly brown in color without distinguishing markings or spurs; apical comb of tibia 3 with rather short thick teeth from anterior to posterior all about the same length. Aedeagus rather wide with sides almost parallel, tapering to a rather abrupt, blunt apex, not curved or twisted, however, slightly arcuate dorsoventrally (Fig. 21); spermatheca as in figures 8–9.

Distribution (Fig. 32): MEXICO. *Sonora*, 52 mi E San Luis, XII-27-60; 51 mi E San Luis, XII-30-60. ARIZONA. *Pima Co.*, (the following locations in Organ Pipe Cactus National Monument) Alamo Wash ½ mi E Hwy. #85, II-23-62; Dos Lomitas, XII-29-60; Headquarters, IX-29-61; 14 mi N Headquarters, II-24-62; 15 mi N Headquarters, X-29-61; Quitobaquito, XII-28-60, X-28-62. *Pinal Co.*, 3 mi NE Apache Junction, XII-4-62. *Maricopa Co.*, Gila Bend, Wickham coll., Picacho, V-1-42, Bryant, and the type locality. UTAH. *Washington Co.*, 15 mi SW Shivwits, VIII-13-62, Ross Hardy coll.; St. George, A. M. Woodbury. NEVADA. *Lincoln Co.*, 10 mi N US #91 on Elgin Road in the Mormon Mountains, V-18-62, Ross Hardy coll.; *Nye Co.*, 19 mi SE Lathrop Wells, III-24-70, and 2 mi SW Mercury, V-25-71. Unless otherwise noted, material was collected by ELS and is in ELSC. Material will be distributed to appropriate institutions. One hundred four specimens were examined.

Intensive collecting has not turned up specimens of *echinus* between Cave Creek, Maricopa County, Arizona and the Washington-Lincoln Counties area of Utah-Nevada, a distance of 240 airline miles.

Remarks: This species is closely related to *unicolor* but can be distinguished by its dorsal seta-like scales and a feeble median carina on the rostrum. The spermatheca is very distinct and shows only a slight variability in form throughout the specimens examined. Parthenogenicity seems to exist in the population in Nevada and Utah as no males have been taken there.

Biology: The specimens from Quitobaquito and 15 mi N Headquarters (Organ Pipe Cactus National Monument) were taken on *Franseria dumosa* and *Franseria* sp. The material from Nye County, Nevada was beaten from an undetermined species of *Franseria* and *Larrea divaricata*. All other material collected by ELS and that collected by Ross Hardy were from *Larrea tridentata*. In the Arizona-Sonoran portion of the range, the adult population is present in largest numbers on

the vegetation in December at which time the females were found to be carrying an average of four mature ova.

***Eucyllus cinereus*, new species**

Figures 10, 10a, 18, 19, 26

Holotype: Female, California, Inyo County, White Mountains, Grandview Public Camp. 8400 ft, VIII-13-64, ELS, ELSC #82. **Allotype:** same data as holotype. Length 3.8 mm, width 1.7 mm; differing in narrow form and with scattered brown scales on dorsum.

Description: Length 4.4 mm; width 2.2 mm; elongate oval; derm mahogany brown; scales and seta-like scales uniformly white giving the body a gray color, no irregular dark patches on dorsum; setae three times as long as broad, erect, truncate at apices, appearing club-like. Rostrum as long as broad, shorter than in other species; feebly sculptured; a feeble indication of a median sulcus extending posteriorly from the epistoma to the anterior margin of the head; punctures on the rostrum moderate in size, oval in shape, rather shallow compared to the other species; scrobes with dorsal and lateral margins reaching orbital of eye channel of scrobe with a feeble median carina converging with orbital of eye, this evident when denuded. Funiculus with second segment one and one-half times longer than third. Prothorax with disc feebly flattened with large deep punctures separated by their diameter and numbering 43.2 per .25 mm²; elytra uniformly gray in color; length of second abdominal sternite not quite as long as three plus four combined, and shape slightly different than occurs in other species; tibia has apical comb with anterior teeth short and thick gradually becoming longer posteriorly until posterior teeth are one-half again as long as anterior teeth while maintaining same thickness. Spermatheca as in figures 10 and 10a.

Paratypes: All 21 are from California, Inyo Co., White Mountains, 9♀ same data as holotype (4 ELSC, 2 FWPC, 1 CASC, 1 LACM, 1 CSLB), 9♀ from type locality, VIII-10-65 (4 ELSC, 1 CASC, 1 LACM, 2 USNM, 1 BYUC); 1♀ type locality, VIII-15-65, M. L. West coll.; 1♀, 7.0 mi S Schulman Grove, 9000 ft, VI-25-63, M. L. West coll.; 1♀, 3.0 mi N Westgard Pass, 7300 ft, VIII-15-64. Length 3.7–4.6 mm (mean 4.0 mm); width 1.5–1.9 mm (mean 1.62 mm). A total of 23 specimens were examined. Unless otherwise noted, the material was taken by ELS and is in ELSC. A few of the paratypes have faint indications of mottling with brown.

Distribution: The range of this species is at present limited to the White Mountains, Inyo County, California (Fig. 32). It would seem probable that it will be encountered in the drier mountain ranges to the east in Nevada, such as the Silver Peak Mountains.

Remarks: This species is generally smaller than

the other species within the genus. *Eucyllus cinereus* can be easily separated from the species by size, coloration, shorter rostrum, seta-like scales, the spermatheca (Figs. 10, 10a), and the aedeagus. Other minor characters aid in defining this species. These are the shape and length of the second abdominal sternite, and the length of the posterior teeth on the apical comb of the tibia 3.

Biology: The specimens from the type locality were taken on *Artemisia tridentata* and *Purshia tridentata*. The other specimens were taken during sweeping of various vegetation types. No mature ova were encountered in the material taken from the period of late June through mid August. The habitat of this weevil is the high Pinyon-Juniper region. The apparent altitudinal range of this species is from 7300–9000 ft; the highest of any in the genus.

***Eucyllus carinarostris*, new species**

Figures 6, 14, 22

Holotype: Female, California, Riverside Co., Pinto Wash Well, II-17-62, 1000 ft. ELS, in ELSC #81.

Description: Length 4.6 mm; width 2.0 mm; elongate oval; derm black, scales dirty white giving body a brownish color; seta-like scales twice as long as broad, recurved, peg-like, and brown in color. Rostrum with strong indication of a median carina extending from epistoma to anterior margin of head; this evident when denuded; a rather deep fovea on each side of the carina with large shallow punctures; rostrum rather strongly sculptured. Funiculus with second segment longer than third, but not twice the length of the third. Disc of prothorax feebly convex with round deep punctures with a mean of 29.7 per .25 mm² spaced approximately their diameter apart. Elytra with a few irregular dark patches, however, mostly uniformly straw colored. Femora with no distinctive markings; tibiae having the apical comb with anterior teeth short and thick, gradually becoming longer towards the posterior margin and closer together while maintaining same thickness. Spermatheca as in figure 6.

Paratypes: All five from California, Riverside Co., 1♀, same data as holotype; 1♀, Joshua Tree National Monument, 7 mi NW Old Dale Junction, I-28-61; 3♀, 5.4 mi NW Old Dale Junction, III-17-61. All material taken by ELS. Length 4.1–5.0 mm (mean 4.4 mm); width 2.0–2.4 mm (mean 2.14 mm). Distribution of paratypes 2 ELSC, 1 FWPC, LACM, 1 USNM. Only six specimens were examined.

Distribution: Apparently limited to the Pinto Wash Well and the old Pinto Lake drainage, Riverside County, California (Fig. 32).

Remarks: This species closely resembles *E. unicolor* but can be readily distinguished by the median rostral carina and the shape of the spermatheca.

Biology: All material was taken on *Larrea tridentata*. Northwest of Old Dale Junction it occurred with *E. vagans*. At Pinto Wash Well it was taken on the same plants with *E. vagans* and *Miloderes* sp.

Eucyllus unicolor Van Dyke

Figures 7, 11, 24, 27

Eucyllus unicolor Van Dyke, 1936, 32. Type locality—"Utah in 1921." (CASC 4145 Ent.). Holotype examined.

Description: Length 4.5–5.0 mm (mean 4.65 mm); width 2.0–2.4 mm (mean 2.09 mm); derm brown to black; scales white, seta-like scales dirty white, no distinct color markings on dorsum; seta-like scales generally twice as long as broad, recurved, rounded at apices. Rostrum with feeble indication of a median fova approximately midway up the rostrum from the epistoma, no indication of a median carina; feebly sculptured, this evident when denuded; punctures on rostrum larger than those on head, but not as large as those found on related species. First segment of funiculus approximately same length as second, third segment slightly shorter than preceding segments. Punctures on prothorax round and rather deep with a mean of 32.4 per .25 mm²; prothorax without distinct marking or patches; the sides not as rounded as in most species. Elytra with no distinguishing marks, uniformly straw color; femora with no distinguishing marks, tibia with apical comb of anterior teeth short, gradually becoming longer posteriorly while maintaining same thickness, posterior teeth not more than one-half again as long as anterior teeth. Spermatheca as in figure 7.

Other type material: One paratype from Westgard Pass, Inyo Co., California, not examined.

Distribution: UTAH. *Washington Co.*, St. George (and vicinity), no other data; Dixie State Park, VII-3-63. NEVADA. *Nye Co.*, 19 mi SE Lathrop Wells, III-24-70. Tanner (1959) reports this species from "St. George, Washington Co., Utah, A. M. Woodbury; Virgin River, Washington Co., Utah, C. J. Weidt, 1892; SW end Cedar Mountains, Toole Co., Utah, W. J. Thomas, VIII-25-53; Peach Springs, Ariz., Ulke, 1896; 'Ariz.'" and again Tanner (1966) from the Nevada Test Site "Area 28 (vicinity of Rock Valley) and . . . Cane Springs." Both of these locations are in Nye County. It is our opinion that this species is confined to western Utah and south central Nevada (Fig. 32). This is based on extensive collecting in southwestern United States and the absence of recently collected, correctly labeled material from other than the locations cited. Numerous snout beetle

specimens have been encountered bearing the label "Peach Springs, Ariz., Ulke" that were apparently mislabeled. Several of these species have been searched for, in vain, in the Peach Springs area. They have been encountered in southwestern Utah and southeastern Nevada. The "Ariz." labeled material gives no real information. This leaves the paratype from "Westgard Pass." This paratype has not been located but it is probably *E. cinereus* which we have previously mentioned resembles *unicolor*. Nineteen specimens were examined.

Discussion: *Eucyllus unicolor* resembles *carinarostris* and *echinus*, but can be readily separated by the length and shape of the setae and the lack of a median carina on the rostrum. The spermatheca is very different from all of the species of the genus (Fig. 7).

Biology: The material examined from St. George was captured on *Larrea tridentata*. Most of the specimens from 19 mi SE Lathrop Wells were on *Franseria* sp.

ACKNOWLEDGMENTS

We wish to thank J. F. Lawrence, Museum of Comparative Zoology, Harvard University, for information on the lectotype of *E. vagans* Horn, and aid in studying the LeConte Collection; Hugh B. Leech, California Academy of Sciences, for use of Academy facilities while working on that collection and for lending material; Ross Hardy, Alan Hardy, Eric M. Fisher, John A. Gruwell, and Sandra L. Jenkins for additional material.

Special thanks are extended to the Superintendents of Joshua Tree National Monument and Organ Pipe Cactus National Monument and their Park Naturalists and Rangers who significantly aided the efforts of the collectors.

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TWO NEW SPECIES OF NORTH AMERICAN FLAT BUGS (HEMIPTERA: ARADIDAE)

NICHOLAS A. KORMILEV¹

ABSTRACT: Two new species of Aradidae are described.

Among unidentified material in the entomological collections of the Natural History Museum of Los Angeles County (LACM), I discovered specimens of the following two undescribed species of Aradidae.

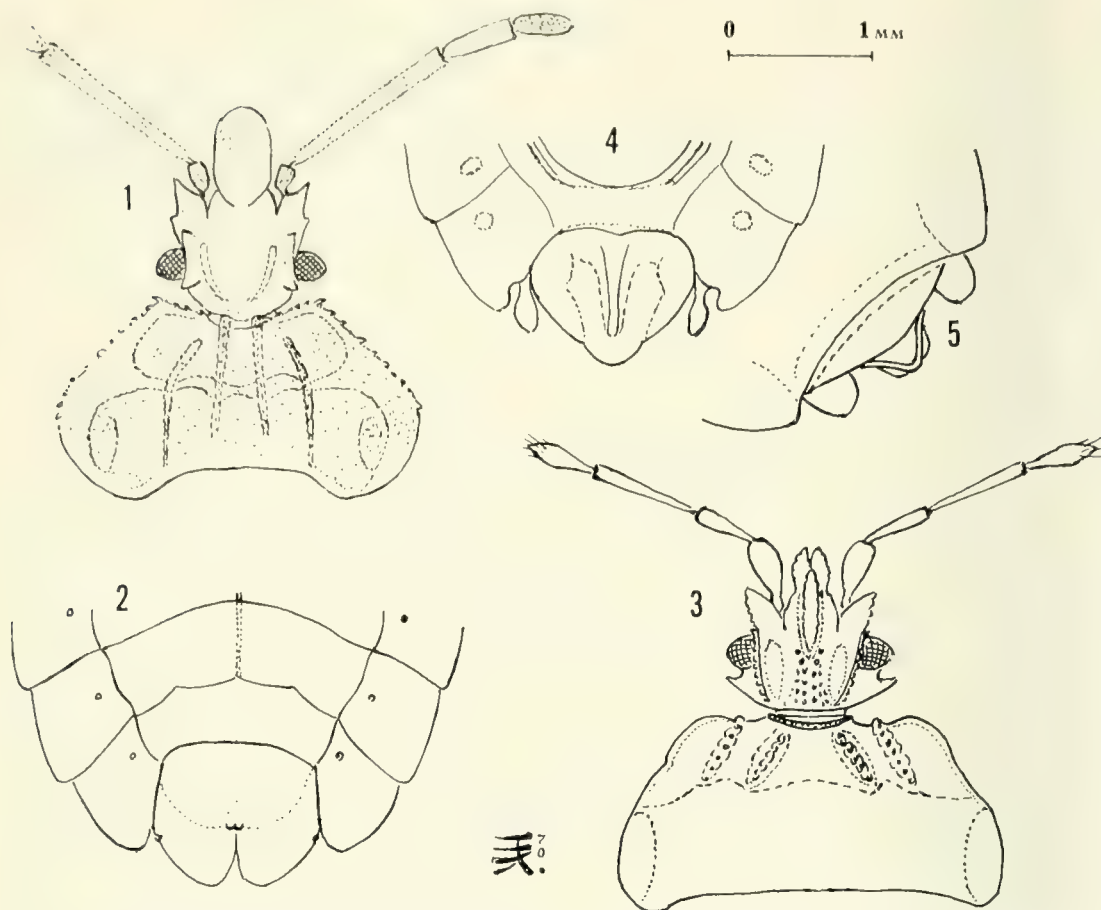
SUBFAMILY ARADINAE GENUS *Aradus* FABRICIUS, 1803

Aradus nevadensis, new species Figures 1-2

Description: Male. Elongate ovate; head, pronotum, and scutellum finely granulate. *Head* longer than its width across eyes (1.27:1); anterior process strong, with parallel sides, reaching basal $\frac{1}{3}$ of antennal segment II; antenniferous tubercles acute, diverging, reaching apical $\frac{1}{3}$ of antennal segment I; lateral tooth small, but distinct; preocular tubercles acute, postocular also acute. Eyes reniform, strongly protruding. Depressions of vertex deep, converging backward in an arc. Antennae slender, almost twice as long as width of head across eyes (1.93:1); antennal segment II narrower than fore femora, gradually dilating toward the tip; relative length of antennal segments I to IV: 1:4.28:1.86:1.14. Labium reaching mesosternum. *Pronotum* less than half as long as its maximum width across middle of lateral borders (1:2.22); the latter strongly convex, rounded; straight and converging anteriorly, and bearing a few small

teeth. Disc raised before and behind deep, transverse depression; inner carinae parallel, very slightly diverging backward. *Scutellum* triangular, longer than its basal width (1.23:1); lateral borders slightly convex at base, then straight; raised. Tip narrowly rounded. Disc raised at basal $\frac{2}{5}$, transversely rugose on apical $\frac{3}{5}$. *Hemelytra* reaching apical $\frac{1}{3}$ of genital lobes; corium expanded and rounded laterally at base, reaching $\frac{1}{2}$ of connexivum V. *Abdomen* ovate; posteroexterior angles of connexiva II to IV not protruding, V and VI slightly protruding, VII forming rounded lobes; inner border of genital lobes slightly diverging behind middle. Sternum VI longer than VII medially (1.2:1). *Color* black to piceous on head, pronotum and scutellum, with exception of latero-posterior borders of pronotum and tip of scutellum, which are white or whitish. Antennal segments I, II, and basal $\frac{2}{3}$ of III, dark brown; apical $\frac{1}{3}$ of III whitish, IV black. Corium of hemelytra ochraceous mottled with whitish, infusate on apical $\frac{2}{5}$; membrane fuscous, whitish at base. Connexivum dark brown with whitish posteroexterior angles and hind borders, the latter with a slight, reddish tinge in middle. Ventral side of body reddish brown, with whitish posteroexterior angles of connexiva. Legs dark brown; coxae and tips of tibiae, whitish. *Size*—total length 7.12

¹ Natural History Museum of Los Angeles, Los Angeles, California. 90007 (Present address: 102-34 93rd Avenue, Richmond Hill, N.Y. 11418).



Figures 1-5. Fig. 1, *Aradus nevadensis*, n.sp., ♂, head and pronotum. Fig. 2, tip of abdomen from below. Fig. 3, *Mezira tropicalis*, n.sp., ♂, head and pronotum. Fig. 4, tip of abdomen from above; ♀. Fig. 5, tip of abdomen from above.

mm; width of pronotum 2.50 mm; width of abdomen 3.25 mm.

Diagnosis: *Aradus nevadensis*, n.sp. is similar to *A. cincticornis* Bergroth (Canadian Ent., 38:198-202, 1906), but it is larger, the head is longer than its width across eyes, antennal segment II is as long as the width of head including both eyes, sternum VI (V visible) is longer than VII (VI visible), and the color is different.

Holotype: Male. California, Nevada Co., Sagehen Creek, 18 June 1962 (R. L. Westcott) LACM.

SUBFAMILY MEZIRINAE

GENUS *Mezira* AMYOT AND SERVILLE, 1843

Mezira tropicalis, new species

Figures 3-5

Description: Male (Female identical except for differences where indicated). Elongate ovate, covered

with a fine, setigerous granulation, with setae extremely short and erect. **Head** slightly shorter than its width across eyes (male 1:1.07, female 1:1.15); anterior process slender, slightly constricted in middle and incised anteriorly, reaching apical $\frac{1}{4}$ of antennal segment I; antenniferous tubercles acute, diverging, reaching basal $\frac{1}{3}$ of antennal segment I; postocular small, acute, reaching outer border of eyes; the latter semiglobose, protruding. Vertex with V-form rows of setigerous granules. Antennae slender, less than twice as long as width of head across eyes (male 1:79:1, female 1:72:1); relative length of antennal segment I to IV: male 1:0.8:1.35:0.7, female 1:0.8:1.4:0.75. Labium reaching hind border of labial groove, the latter closed posteriorly. **Pronotum** trapezoidal, shorter than its maximum width (male 1:1.92, female 1:2.12); fore lobe is narrower than hind lobe (male 1:1.35, female 1:1.42); collar thin, straight anteriorly; anterolateral angles rounded, slightly expanded and reflexed, produced forward as far as collar;

lateral border parallel at humeri, converging and barely sinuate anteriorly; hind border almost straight. Fore disc with 4(2+2) high, granulate ridges; hind disc granulate; interlobal depression deep. *Scutellum* shorter than its basal width (male 1:1.30, female 1:1.42); lateral borders thinly carinate and slightly sinuate on apical half; tip rounded; disc with a thin median carina, areas laterad of latter granulate. *Hemelytra* reaching beyond fore border of tergum VII (δ), or reaching hind border of tergum VI (η); apical angle of corium blunt, apical border convex, rounded. *Abdomen* ovate, longer than its maximum width across segment IV (male 1.33:1, female 1.41:1); connexivum wide and slightly raised laterally; posteroexterior angles of the connexiva II to VI slightly protruding, blunt; those of VII produced backward as rounded lobes, reaching $\frac{1}{2}$ of paratergites (δ), or rounded, reaching $\frac{1}{2}$ of tergum IX (η). Paratergites (δ) thin, clavate, reaching apical $\frac{1}{3}$ of hypopygium; the latter cordate, with a thin median ridge, slightly shorter than disc of hypopygium. Paratergites (η) large, rounded, reaching apical $\frac{1}{4}$ of slightly tricuspidate segment IX. Spiracles II to VII ventral, placed far from margin, VIII also ventral, but placed closer to margin and not visible from above. *Legs* unarmed. *Color* dark ferrugineous, connexivum

and venter ferrugineous. *Size*: total length: male 7.78, female 8.67 mm; width of pronotum: male 2.83 mm; female 2.83 mm; width of abdomen: male 3.56 mm; female 3.56 mm.

Diagnosis: *Mezira tropicalis*, n. sp. is closely related to *M. mexicana* Kormilev. (Proc. United States Nat. Mus., 119:245-258, 1964), from Vera Cruz, Mexico, but is larger, with the anterior process of the head longer and more slender; antennal segment III relatively longer, almost twice as long as IV and paratergites (η) longer, reaching to the apical $\frac{1}{4}$ of segment IX.

Holotype: Male. Mexico, Jalisco, 13 mi W Atenquique, 7800 ft, 13 July 1966 (J. R. Dixon and W. R. Heyer) LACM. *Allotype*: Female, 1 female paratype and 5 nymphs, same data as holotype.

ACKNOWLEDGMENT

For the privilege of studying the Aradidae in the collections of the Natural History Museum of Los Angeles County, I express my sincere thanks to Charles L. Hogue, Senior Curator of Entomology.

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A NEW SPECIES OF AMBUSH BUG FROM ARIZONA (HEMIPTERA: PHYMATIDAE)

NICHOLAS A. KORMILEV¹

ABSTRACT: A new species of macrocephaline ambush bug from Arizona is described.

The ambush bugs are represented in the continental United States by two subfamilies, Phymatinae and Macrocephalinae. The first is common throughout the country, but the second is rather rare, being distributed mainly in the south and southwest, although *Macrocephalus prehensilis* (Fabricius), 1803, has been recorded as far north as Kentucky and Kansas (Evans, Ann. Ent. Soc. America, 24:711-736, 1931). While examining specimens of the latter subfamily in the collection of the Natural History Museum of Los Angeles County (LACM) and in a lot sent to me by T. Halstead, I found a few specimens of

an undescribed *Macrocephalus*, collected in Arizona.

In the description all measurements are given in millimeters. The first figure in a ratio represents the length and the second the width of the measured part. The length of the abdomen was measured from the anteroexterior angles of connexivum II to the tip of abdomen.

¹ Natural History Museum of Los Angeles County, Los Angeles, California. 90007 (Proc. United States Nat. Mus., 119:245-258, 1964), from Vera Cruz, Mexico, but is larger, with the anterior process of the head longer and more slender; antennal segment III relatively longer, almost twice as long as IV and paratergites (η) longer, reaching to the apical $\frac{1}{4}$ of segment IX. 102-34 93rd Avenue, Richmond Hill, N.Y. 11418).

SUBFAMILY MACROCEPHALINAE
GENUS *Macrocephalus* SWEDERUS, 1787

Macrocephalus similis, new species

Figure 1

Description: *Female.* Elongate ovate; head, fore lobe of pronotum and corium, finely granulate; connexiva II roughly granulate. **Head** almost twice as long as its width across eyes (1.60:0.92); antocular portion narrower than postocular (0.64:0.80); ocelli placed nearer hind border of head than eyes (0.24:0.28); upper lobe of genae rounded, lower angular; bucculae evenly rounded and granulate on border; lateral borders of labial groove also granulate. Antennae almost as long as head (1.56:1.60); antennal segment I subtriangular, flattened laterally; II almost globose, III evenly enlarged toward tip, IV fusiform; relative length and width of antennal segments I to IV: 0.40:0.32 — 0.24:0.20 — 0.28:0.16 — 0.64:0.36. Labium reaching middle of prosternal cavity. **Pronotum** shorter than its maximum width across humeri (2.28:3.04); fore lobe narrower than hind lobe (1.52:3.04). Anterior angles dentiform, acute, directed forward; anterior border deeply sinuate; anterolateral-anterior borders slightly convex, diverging backward; interlobal notch sinuate; anterolateral-posterior borders convex, rounded; lateral angles incised as in *M. cimicoides* Swederus, 1787; posterolateral borders firstly convex, then sinuate; hind border convex in middle. Fore disc convex, finely granulate, more densely granulate along lateral borders; pronotal pit elongate. Hind disc roughly punctured, punctures forming a net-like surface and are larger anteriorly and laterally. Pronotal carinae short, stout anteriorly, diverging, tapering and evanescent posteriorly, without any knob or ridge anteriorly. **Scutellum** twice as long as its maximum width (110:55), with a thin median carina, which is enlarged on basal 1/7. Disc roughly punctured at base laterally, finely punctured elsewhere on disc, the basal portion moderately inflated and with a weak, ivory-like elevation in the form of a 3-pronged spear-head on basal half medially, more distinct in the males. **Hemelytra** reaching tip of abdomen; corium finely granulate, granules arranged in groups. **Abdomen** cordate, slightly longer than its maximum width across segment III (4.12:4.00); posteroexterior angles of connexiva barely protruding; connexiva II covered with a rough and dense granulation; other connexiva sparsely and finely granulate along exterior border. **Legs** with fore coxae cylindrical, without knob or tooth, but roughly granulate inferiorly. Fore femora longer than wide (2.16:0.88), convex exteriorly and with a row of rough, setigerous granules on upper side. Fore tibiae without tarsi. Middle and hind femora with rough, setigerous granules on upper and lower sides, with smaller granules laterally; middle and hind tibiae densely granulate. **Color**

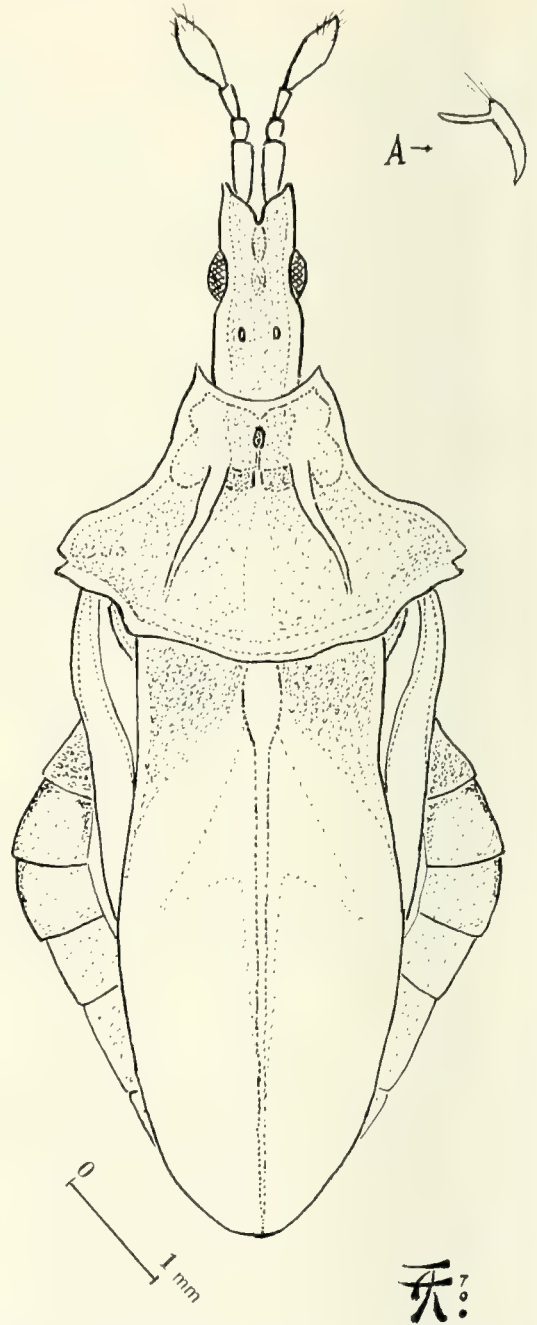


Figure 1. *Macrocephalus similis*, n.sp., holotype (female), dorsal aspect; A—paratype (male), right paramere.

grayish brown; head on upper side medially, fore lobe of pronotum in middle, and exterior borders of connexiva III and IV, black or blackish; rest of fore lobe of pronotum and connexiva III and IV, reddish brown; antennae, pronotal carinae, scutellar carina

and inflated portion of disc, and connexiva II, ochraceous or slightly brownish; anterolateral portions of scutellum (roughly punctured) brown; ventral side of body ochraceous, brownish on fore femora, coxae, middle and hind femora, and venter laterally and posteriorly; middle tarsi black, hind tarsi greenish-yellow. *Size*—total length 8.16 mm; width of pronotum 3.00 mm; width of abdomen 4.00 mm.

Male. Smaller and more slender than female, more densely granulate and with color generally darker; upper surface of head black; antennae, pronotum and scutellum, with exception of a three-pronged, spear-shaped ivory spot, black mottled somewhat with yellow; connexiva III, IV and most of V, black; ventral side of the body yellow with some brown stripes on fore femora and venter laterally; reddish brown near lateral angles of venter. One male is colored as the females.

Measurements: Head 1.60:0.90; relative length and width of antennal segments I to IV: 0.48:0.22 — 0.22:0.20 — 0.32:0.20 — 0.80:0.32; pronotum 2.20:3.08, ratio width of fore lobe: width of hind lobe as 1.60:3.08; scutellum 4.20:2.20; abdomen 4.16:3.60 (across segment III); fore femora 2.0:0.9. Paramere is of *Macrocephalus* type.

Size: Total length 7.92 mm; width of pronotum 3.08 mm; width of abdomen 3.60 mm.

Diagnosis: *Macrocephalus similis*, n.sp. is very similar to *M. barberi* Evans, 1931, from California,

and probably was confused with the latter, but may be separated from it by larger size, pronotal without knob or ridge anteriorly, granulation pronotum and connexivum generally finer and not dense, head relatively shorter, pronotum relatively longer, and abdomen slightly longer than its maximum width.

Holotype: Female. Arizona, Cochise Co., 5 mi W Portal, 25 June 1959 (L. A. Stange) LACM. *Allotype*: Male. Arizona, Santa Cruz Co., Pena Blanca Lake, 22 May 1970 (T. Halstead) LACM.

Paratypes: 5 ♂ and 7 ♀, some were collected with the allotype, and others in the same locality on 15 November 1969. T. Halstead coll. Deposited in the Natural History Museum of Los Angeles County and in the collections of Department of Entomology, University of Arizona, Tucson, and of the author.

ACKNOWLEDGMENTS

For the privilege of studying Phymatidae in the collection of the Natural History Museum of Los Angeles County, I express my sincere gratitude to Charles L. Hogue, Senior Curator of Entomology. I am also indebted to T. Halstead, Phoenix, Arizona, for the gift of Phymatidae collected by him in Arizona.

Accepted for publication November 16, 1971.

THE ASCIDIANS *STYELA BARNHARTI*, *S. PLICATA*, *S. CLAVA*, AND *S. MONTEREYENSIS* IN CALIFORNIAN WATERS

DONALD P. ABBOTT¹ AND JEFFREY V. JOHNSON²

ABSTRACT: Reexamination of the holotype of *Styela barnharti* Ritter and Forsyth, 1917, shows that it is *Styela plicata* (Lesueur, 1823). The species designated *Styela barnharti* by Van Name (1945) and subsequent authors is *Styela clava* Herdman, 1881, an asiatic form probably introduced into Californian waters in the late 1920's. The latter species is distinct from the native west coast form *Styela montereyensis* (Dall, 1872).

The stalked simple ascidian usually referred to as *Styela barnharti* is common on floats and pilings in protected coastal waters of southern California (Ricketts and Calvin, 1968; MacGinitie and MacGinitie, 1968). In some harbor areas it is found with another stalked form, *Styela montereyensis*; the two are not always easily distinguished, especially when overgrown by hydroid and bryozoan colonies.

Van Name (1945) expressed the opinion that the original description of *S. barnharti* by Ritter and Forsyth (1917) gave "a very poor idea of the size and usual character of the species," and pro-

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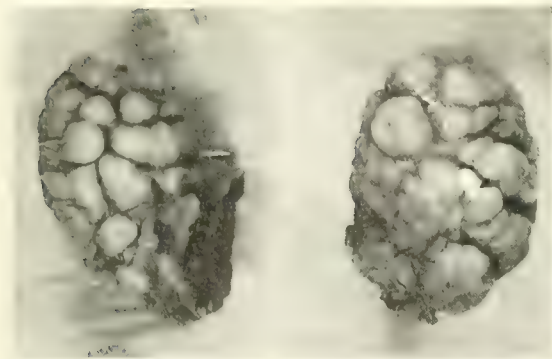


Figure 1. Holotype of *Styela barnharti* (= *S. plicata*); positions of apertures marked in right hand view.

vided a new description. Subsequent investigators have found it difficult to reconcile Ritter and Forsyth's original description of *S. barnharti* with the features of the species called *S. barnharti* by Van Name. J. R. Whittaker (pers. comm., 1971) called our attention to the fact that Ritter and Forsyth's figure of the intact holotype actually resembles another Californian ascidian (not named), and suggested that the *S. barnharti* of Van Name (1945) might be merely a shorter-stalked variety of *S. montereyensis*.

In the present paper we show: (1) the holotype of *Styela barnharti* Ritter and Forsyth, 1917, is a specimen of *S. plicata* (Lesueur, 1823); (2) the entity called *S. barnharti* by Van Name (1945) and subsequent authors is actually *S. clava* Herdman, 1881; and (3) the latter species is quite distinct from the Californian stalked ascidian *S. montereyensis* (Dall, 1872).

THE HOLOTYPE OF STYLELA BARNHARTI RITTER AND FORSYTH, 1917, AND COMPARISON WITH *S. PLICATA* (LESUEUR, 1823)

The holotype of *S. barnharti* was discovered recently at Stanford University, and is now deposited in the Department of Invertebrate Zoology, California Academy of Sciences (CASIZ Type Series No. 552). It has been reexamined by the senior author. In external features the tunic (Fig. 1) closely resembles Ritter and Forsyth's fig. 2, pl. 38. The body within the tunic exists in several pieces but most of the parts are present and it has been possible to verify nearly all of Ritter and

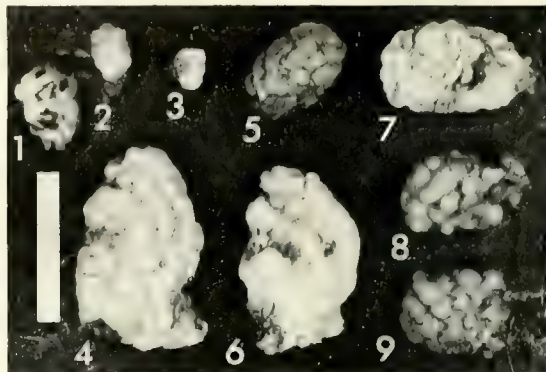


Figure 2. *Styela plicata* from different localities. 1-4, San Diego, California. 5, holotype of *S. barnharti*, San Diego, California. 6, Long Beach, California. 7, Newport Bay, California. 8-9, Cedar Key, Levy Co., Florida.

Forsyth's recorded observations. The following account corrects a few details and adds others not included in the generally adequate original description.

Branchial tentacles.—"Of several sizes, about forty," according to Ritter and Forsyth. Reexamination shows 64, of 3 orders (but of 4 sizes, as some third order tentacles are very small), fairly regularly arranged in the pattern 1-3-2-3-1.

Internal longitudinal vessels.—A recount on the type, taken across the middle of the pharynx, shows the following distribution (DL = dorsal lamina, vessels on branchial folds in parentheses):

Right	4(19)8(21)7(16)8(14)4
DL	
Left	5(20)6(20)7(21)4(21)2.

Ritter and Forsyth found 94 and 102 vessels, on right and left, respectively; we found 101 and 106. The discrepancies found probably reflect a difference in the level on the pharynx at which the counts were taken, and differences in assignment of vessels near the bases of folds to branchial folds or interfold areas; they are not considered significant.

Gut.—In cross section the stomach showed 33 folds; Ritter and Forsyth found about 35. The presence of numerous endocarps on the intestine is confirmed.

Testes.—These are considerably more numerous and the larger testes more complexly branched (Fig. 5) than is indicated in Ritter and Forsyth's illustrations (their figs. 39 and 40, pl. 42), though no testes exhibit such attenuated branches as those



A



B

Figure 3. A, *Styela clava*, San Diego, California. B, *Styela montereyensis*, Monterey, California.

shown for an old and large individual of *S. plicata* by Van Name (1945:295, fig. 192).

The holotype has been compared directly with individuals of *Styela plicata* from several localities (see below). In external features (Figs. 1–2) and in all internal qualitative features, the holotype is a “typical” specimen of *S. plicata* (compare Fig. 8C, this paper, with Ritter and Forsyth’s figs. 39 and 40, pl. 42). The quantitative characteristics, both those which increase more or less regularly with body size (e.g., number of internal longitudinal pharyngeal vessels) and those which do not (e.g., number of ovaries, number of plications in the stomach wall), are found in figure 6. In most of these features the holotype of *S. barnharti* is not an exceptional specimen of *S. plicata*. The number of gonads (9 on the right side, 3 on the left) is rather large (Van Name, 1945, records 4–7 on the right and 2 on the left as more usual), but it is

within the known range of *S. plicata*. The species; Tokioka (1953:268) reported 1–3 on the right and 1–3 on the left in Japanese specimens, and Tucker (1942) recorded 2–11 on the right and 1–3 on the left in individuals from North Carolina.

The first correct published record of the occurrence of *S. plicata*, under that name, on the west coast of North America is that of Reish (1963), based on material collected in the spring of 1960 at Alamitos Bay, Long Beach, California, and determined by one of us (Abbott). An earlier report of *S. plicata* from Point Richmond, San Francisco Bay (Abbott, 1954) is erroneous; re-examination of the specimens shows they are *S. clava*. New records of *S. plicata* in southern California are given by Fay and Johnson (1971). It is now clear that *S. plicata* was present at San Diego at least as early as July 1915, when Ritter and Forsyth’s material was collected. Its present known distribution on this coast extends only from San Diego to Santa Barbara, California, at depths of 0–3 m. Elsewhere it is widely distributed in the Atlantic, Pacific, and Indian Oceans, and has been the subject of numerous field and laboratory investigations.

Specimens examined: Point Loma, San Diego, California, 24 November 1971, coll. G. Lingle; Mission Bay, San Diego, California, 7 August 1966, coll. K. M. Taylor; Newport Bay, California, autumn 1966, coll. G. Bane; Alamitos Bay, Long Beach, California, 18 August 1960, coll. D. J. Reish; Cedar Key, Levy Co., Florida, 21 August 1950, coll. K. C. Strawn; Boca Ciega Bay, Pinellas Co., Florida, 3–28 November 1955, coll. R. F. Hutton; Beaufort, North Carolina, 13 December 1915, coll. unknown; and Wakanoura, Kii, Japan, no date, coll. Jordan and Snyder.

REEXAMINATION OF THE *STYELA BARNHARTI* OF VAN NAME (1945)

Van Name (1945) presents the first unequivocal published account of this species on the west coast. We have examined specimens from eleven different localities (see below). An especially large series from Venice, California was examined in connection with studies of reproduction and growth (J. V. Johnson, 1971). Most animals were taken intertidally or in the shallow subtidal zone, on floats, pilings, or rocks; only the specimen from the Hyperion sewer outfall comes from greater depths (50 ft).

Van Name’s description of *S. barnharti* is

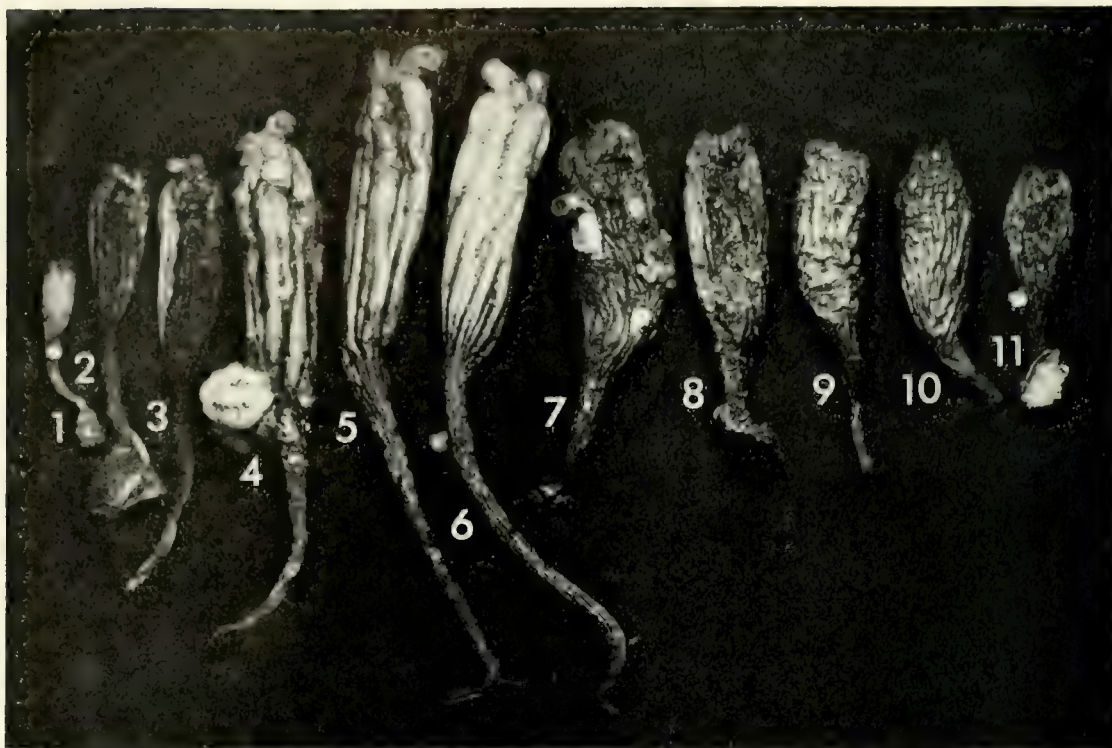


Figure 4. Styelid ascidians found growing together, Santa Barbara harbor, California. 1-6, *Styela montereyensis* (specimen 4 bearing an *S. plicata*). 7-11, *Styela clava*.

where it deals with the placement of the stomach and intestine, is generally accurate, though it does not always convey the range of variation to be expected. The following account augments or modifies only those portions of the description which require this.

External features.—Our largest specimens reached a total length of about 200 mm. Length of the stalk seldom approaches half the total length, and may be less than one tenth the total length, or virtually absent in small specimens. Division between body and stalk ranges from sharp to very gradual and indistinct. Number and distribution of tubercles on the test varies greatly; at the extremes they may cover as much as the anterior two thirds of the body proper, or they may be confined to a few small bumps about the apertures. Development of longitudinal wrinkles likewise varies greatly, but the longitudinal ridges and grooves, when present, represent folds in the relatively thin and leathery tunic, and not alternating areas of thick and thin tunic. The oral siphon may point anteriorly or be canted at a slight angle, but it never recurves to point posteriorly as it usually does in *S. montereyensis*.

Dorsal tubercle.—The aperture often shows greater inrolling of the horns, and greater irregularity, than indicated by Van Name (1945); specimens exhibit the same sorts of variations depicted by Millar (1960, fig. 1 B-D) for *S. clava*.

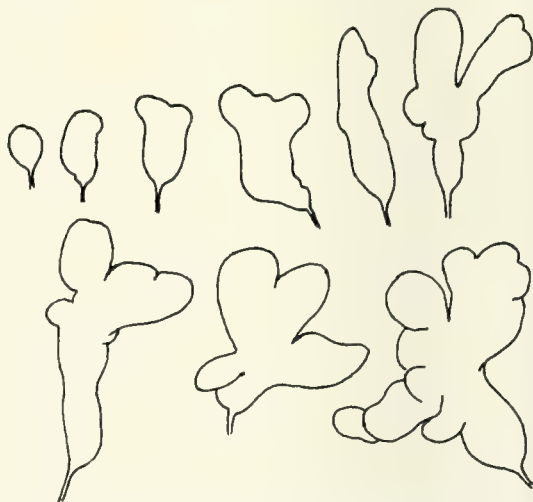


Figure 5. Outlines of testes from holotype of *Styela barnharti* (= *S. plicata*), showing nature of branching.

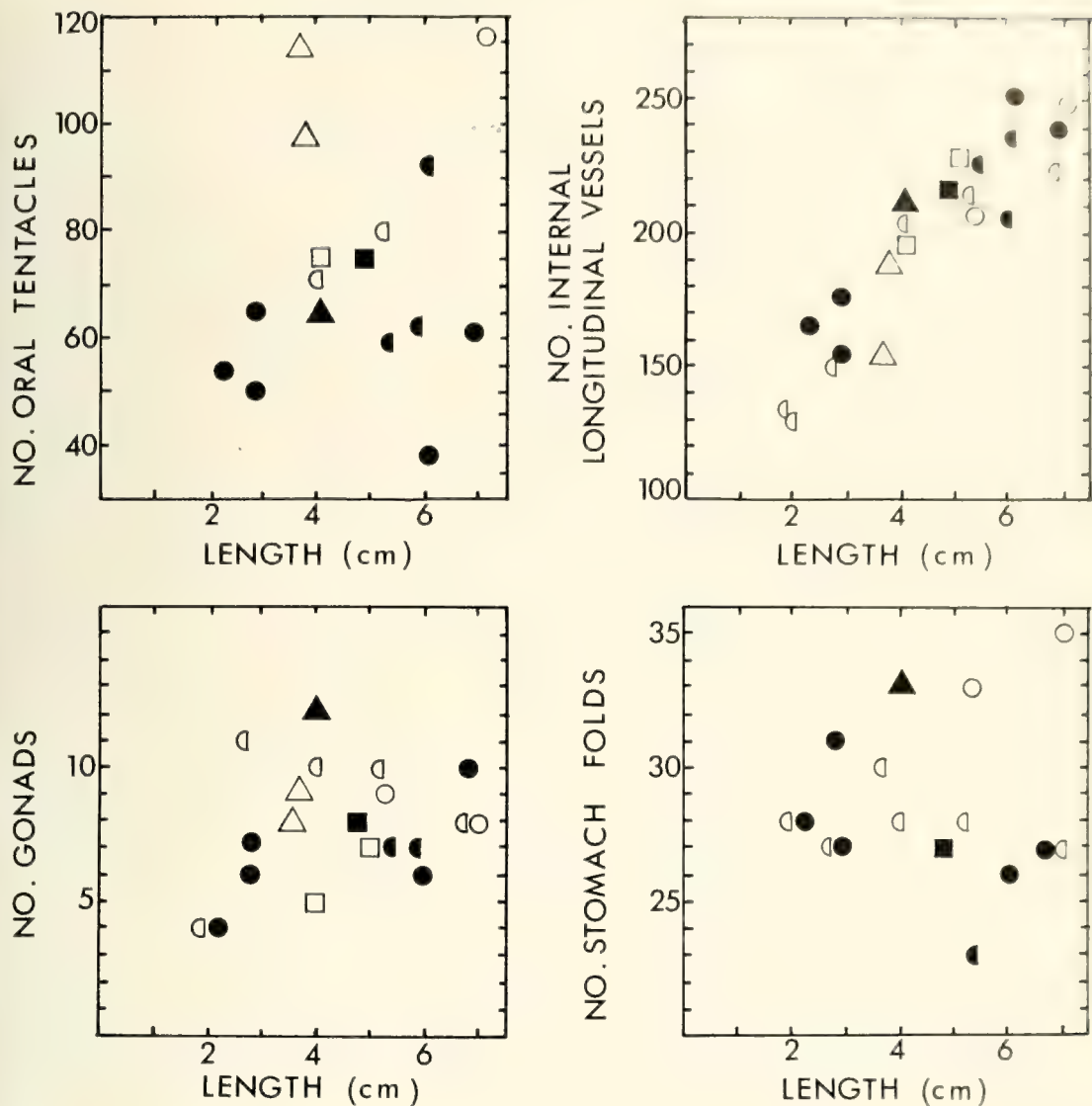


Figure 6. *Styela plicata*; relation of total length (body and stalk) to numbers of oral tentacles, internal longitudinal vessels, gonads (ovaries), and plications on stomach wall.

Tentacles.—Average number 55 in 7 individuals counted; range 44 (in a specimen 135 mm long) to 76 (in a 90 mm individual).

Pharynx.—The pharyngeal folds are low but

bear closely crowded internal longitudinal vessels whose number increases with body size. Total number of internal longitudinal vessels (on both sides) ranged from 137 in an animal 135 mm long to

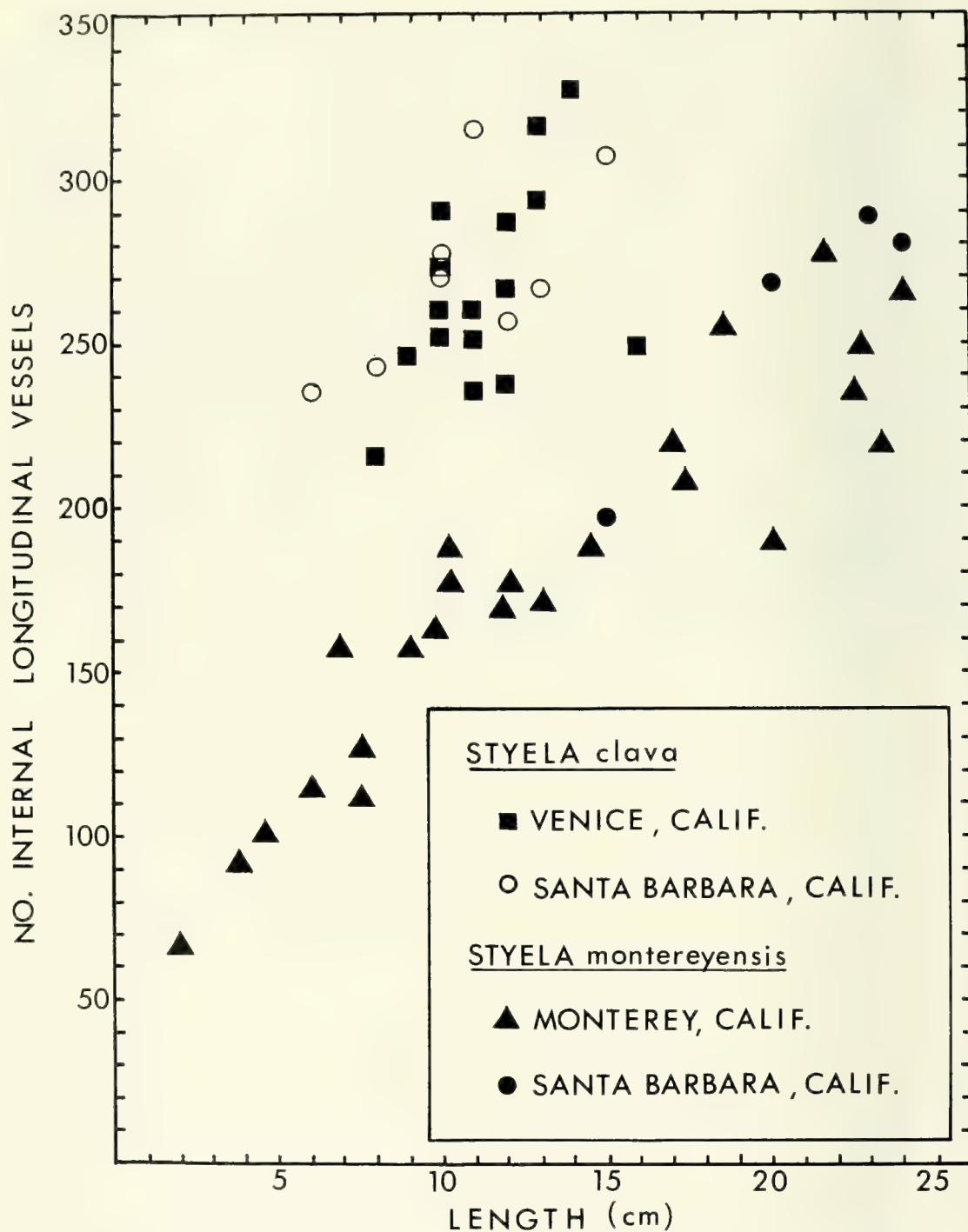


Figure 7. *Styela clava* and *S. montereyensis*; relation between total length (body and stalk) and number of internal longitudinal vessels on pharynx.

TABLE 1. Distinguishing features of *Styela clava* and *Styela montereyensis*.

Feature	<i>S. clava</i>	<i>S. montereyensis</i>
Tunic	Usually with conspicuous tubercles, at least anteriorly (Figs. 3A, 4). Longitudinal folds absent to well-developed, confined mainly to posterior body and stalk, consisting of wrinkles in tunic rather than structural folds (Figs. 3A, 4).	Tubercles lacking, or few and inconspicuous; larger animals with a few loose warts of tunic material, easily detached, adhering near the siphons (Figs. 3B, 4). Longitudinal ridges and grooves on body and stalk extending anteriorly nearly to siphon and representing respectively thicker and thinner regions of the test (Figs. 3B, 4).
Siphons	Both siphons straight, directed anteriorly (Fig. 4).	Oral siphon curved, directed ventrally or posteriorly (Figs. 3B, 4).
Pharynx	Esophageal aperture located halfway down pharynx; branchial folds with numerous internal longitudinal vessels (Fig. 7).	Esophageal aperture located near posterior end of pharynx; branchial folds with fewer internal longitudinal vessels (Fig. 7).
Gut	Stomach in descending position (Fig. 8A); first intestinal loop near posterior end of body; intestinal wall bearing numerous endocarps.	Stomach in ascending position (Fig. 8B); first intestinal loop about halfway up body; intestinal wall smooth, without endocarps.
Atrial tentacles	Forming more than one row.	Forming only a single file.
Ovaries	Tubular, typically 4-9 on the right and 2-5 on the left, one or more often branched posteriorly (Fig. 8A).	Tubular, typically 2 on each side (rarely 1 or 3), seldom branched posteriorly (Fig. 8B).
Testes	Clustered into compact lobes (Fig. 8A).	Individual testes separate, simple or branched, not clustered into lobes (Fig. 8B).
West coast distribution and habitat	San Diego Bay to San Francisco Bay, California; in areas not exposed to strong surf; low intertidal to at least 75 ft depth.	San Diego Bay, California to British Columbia; on outer coastal rocks and pilings but also invading calmer harbors; low intertidal to about 100 ft depth; coexists with <i>S. clava</i> at Santa Barbara and Mission Bay, San Diego.

to 327 in a specimen 140 mm long. Distribution of vessels in 3 animals exhibiting low, intermediate, and high vessel counts were as follows:

	Total	Length
-Right	2(16)1(16)2(14)4(10)3	
DL		25 mm
-Left	4(16)3(12)3(14)3(11)3	
-Right	6(35)4(31)3(31)5(21)4	
DL		100 mm
-Left	6(30)4(29)7(26)7(17)4	
-Right	4(44)6(36)4(42)5(24)3	
DL		140 mm
-Left	6(35)4(36)4(43)5(22)4.	

The esophageal opening occurs about halfway down the pharynx. One would never infer this from Van Name's figure 205, though he correctly notes that the dorsal lamina "extends far behind the esophageal opening."

Gut (Fig. 8 A).—The esophagus and stomach descend posteriorly from the esophageal opening, and the stomach is always in a descending position. Beyond its pyloric end the intestine curves sharply anteriorly again and extends toward the base of the atrial siphon. In relaxed specimens the intestine shows little curvature; in contracted animals it may bend, even rather sharply, where it passes the esophageal region. In none of the specimens examined by us was the placement of esophagus and stomach and the course of the intestinal loop at all similar to the situation portrayed by Van Name (1945:310, fig. 205).

Gonads (Fig. 8 A).—Van Name (1945) found 5-9 ovaries on the right and 3-5 on the left. We find 4-9 (average 6) on the right and 2-5 (average 4) on the left in a series of 26 individuals 25-160 mm in total length. Most specimens have at least one ovary which is branched poste

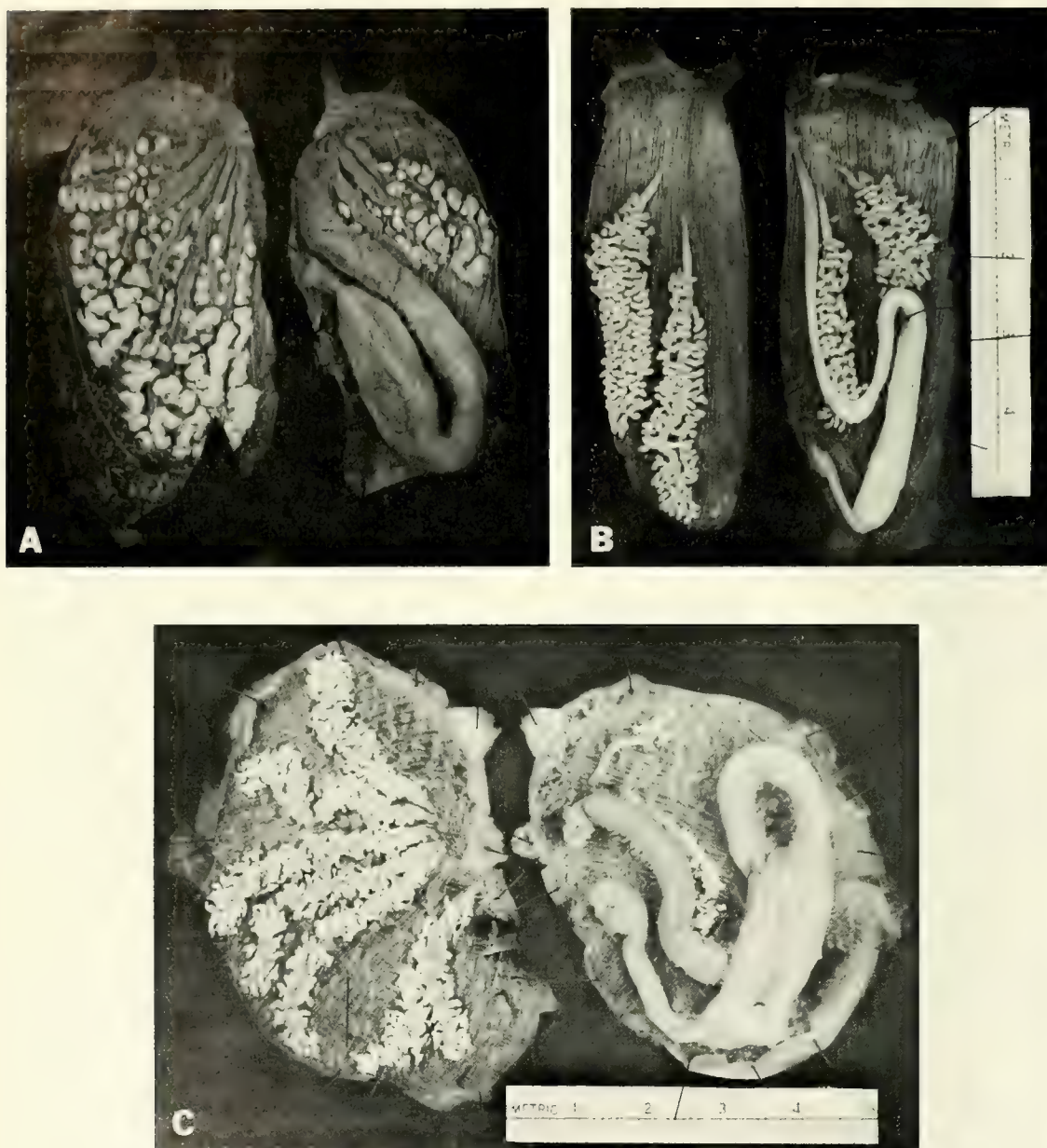


Figure 8. Medial views of right and left halves of body with pharynx removed, showing gut and gonads. A, *Styela clava*, body as shown 70 mm long. B, *Styela montereyensis*. C, *Styela plicata*.

such ovaries were counted as single ovaries. Testes are grouped in tight clusters, as described and figured by Van Name.

Atrial tentacles.—Minute, forming a narrow band several tentacles in width, circling the interior base of the atrial siphon. The condition is similar to that shown by Tokioka (1955b, fig. 3) for *Styela clava* from Japan, but instead of two

distinct rings of tentacles separated by a bare strip, the area between the rings is also occupied by tentacles.

Through the courtesy of David Pawson and Maureen Downey it was possible to examine several specimens of *Styela clava* Herdman, 1881 in the collections of the U. S. National Museum of Natural History, taken near the type locality

(Kobe, Honshu, Japan; USNM 11703); these animals had been examined and identified previously by Tokioka (1967:191). Test tubercles in these Japanese specimens are somewhat more sparsely and regularly placed than is typical of Californian individuals, but this is a character in which both American and Asiatic populations show enormous and widely overlapping variation. A slight difference exists in the atrial tentacles, as noted earlier. In all other respects the species dealt with by Van Name under the name *Styela barnharti* agrees with the Japanese specimens and with recent descriptions of *Styela clava* (Millar 1960; Tokioka 1953, 1959, 1967; Rho 1971).

The source of Van Name's curious figure of the gut (1945:310, fig. 205) remains a mystery. Harold S. Feinberg placed at our disposal the earliest Californian collection of *S. clava* in the American Museum of Natural History, New York (AMNH 931, taken in Newport Bay on 15 November 1933 by G. E. MacGinitie, and noted on the label to "occur abundantly on piles, etc."). The specimens, mostly dissected already, had been identified by Van Name as *S. barnharti*. All are typical *S. clava* as regards the gut and other features. A search through the other collections of *S. barnharti* in the American Museum which had been examined and identified by Van Name, failed to reveal a specimen designated as the source of the figure in question. There is a possibility that in making the drawing Van Name removed the gut and sketched it by itself, in an unnatural position; one specimen in lot AMNH 931 has the gut wholly separated from the body, and it can be twisted to resemble that in Van Name's figure. At any rate, the figure is either inaccurate or portrays an individual with a grossly distorted or aberrant gut.

Styela clava is widely distributed on Asiatic shores, ranging from the Kurile Strait, Sea of Okhotsk, through southern Siberia, Japan, Korea, and the China coast at least as far south as Shanghai. It was discovered in the vicinity of Plymouth, England in 1953, where it was described as a new species (*Styela mammiculata* Carlisle, 1954). Carlisle noted its similarity to the *Styela barnharti* of Van Name (1945), and its identity with *S. clava* was shown by Tokioka (1955a) and Millar (1960). Clearly a recent introduction here, it has now spread to other parts of southern England (Millar, 1970), and the French channel coast (Monniot, 1970).

In Californian waters *S. clava* is regularly abundant in sheltered areas from San Diego to Santa

Barbara (Fay and Johnson, 1971). North of Point Conception its occurrence is more sporadic. It is recorded once from Morro Bay, and in most years from Monterey Bay. It can be found in most years in San Francisco Bay, though populations in some localities disappear after period of heavy rains (W. E. Berg, Charles Spowart pers. comm.). The species has never been noted in either Tomales Bay or Bodega Bay to the north of San Francisco (W. B. Gladfelter and C. H. Hand, pers. comm.), despite the seeming suitability of the habitat and extensive collecting by field biologists.

Specimens examined from: Point Loma, San Diego, California, 24 November 1971, coll. G. Lingle; Mission Bay, San Diego, California, 15 June 1959, coll. J. H. McLean, and 10 August 1966, coll. K. M. Taylor; Newport Bay, California, 15 November 1933, coll. G. E. MacGinitie; Hyperion sewer outfall, Palos Verdes Peninsula, Los Angeles, California, 10 April 1971, coll. W. J. North; Venice, Santa Monica Bay, California, various dates in 1971, coll. R. C. Fay; Santa Barbara, California, June 1971, coll. R. C. Fay; Morro Bay, California, 4 February 1972, coll. D. H. Montgomery; Monterey, California, 15 November 1961, coll. D. P. Abbott; Oakland, San Francisco Bay, California, 26 April 1955, coll. R. Rinaldi; Berkeley, San Francisco Bay, California, 20 April 1955, coll. R. Rinaldi; Point Richmond, San Francisco Bay, California, 12 June 1949, coll. R. Shaw.

COMPARISON OF *S. CLAVA* AND *S. MONTEREYENSIS*. AND THE INTRODUCTION OF *S. CLAVA* TO CALIFORNIA

Styela clava can usually be distinguished from *S. montereyensis* by its shorter stalk, plumper body, and possession of tubercles anteriorly. Variation in all of these features is great, and occasional specimens are found which are difficult to identify in the field. Internally the species are unquestionably quite different, and no specimens have been examined by the authors, or reported by others, whose features suggest hybrid origin. The most useful characters distinguishing the two species are shown in table 1.

Information now available permits a reasonable guess as to the date *S. clava* was introduced into Californian waters. Ritter collected ascidians intensively over a period of two decades from

1917, especially in southern California, and it seems unlikely he could have missed this species had it been common in his time. It is also unlikely that Ritter mistook it for *S. montereyensis*. He mentions taking the latter "from many points on the coast from San Diego to Mendocino" (Ritter and Forsyth, 1917:451), and the accompanying description and figures of *S. montereyensis* clearly apply to that species alone. We conclude that *S. clava* was absent (or at least extraordinarily scarce) in Californian waters prior to 1917.

No species resembling *S. clava* is reported by Johnson and Snook (1927), though these authors, too, collected extensively in areas where *S. clava* is now abundant, and were familiar with *S. montereyensis*. Johnson had worked with ascidians under Ritter (Ritter, 1909:66) and would probably have spotted the difference between *S. clava* and *S. montereyensis*. Ricketts and Calvin (1939) mention only *S. montereyensis*, but their figure 107 almost certainly depicts *S. clava* (see also Van Name, 1945:310). In any event, *S. clava* was on the coast by that time, as documented by the collections of MacGinitie in 1933 at Newport Bay (cited above). George and Nettie MacGinitie, who arrived at the Kerckhoff Marine Laboratory in 1932, inform us (pers. comm.) that *S. clava* also was abundant in Newport Bay in 1932 and all subsequent years, and that *S. montereyensis* has never been common there. We conclude that *S. clava* probably gained its foothold on the Californian coast in the late 1920's.

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RESEARCH NOTES

A NEW SPECIES OF *PUGNUS* FROM COCOS-KEELING ISLANDS, INDIAN OCEAN (GASTROPODA)

The littoral molluscan fauna of Cocos-Keeling Islands, isolated atoll group of the eastern Indian Ocean, was catalogued by Maes (Proc. Acad. Nat. Sci. Philadelphia, 119(4):93-217, 1967), and its geographic affinities assessed. Included in the collections which formed the basis of that report were several specimens of an undescribed species of *Pugnus*, a peculiar gastropod which may be an aberrant member of the Marginellidae, a family under study by the author. Through the kindness of Virginia Orr Maes, Academy of Natural Sciences, Philadelphia, and Winston F. Ponder, The Australian Museum, I have had the opportunity to compare the Cocos-Keeling specimens with specimens of the Australian *Pugnus parvus* Hedley (Rec. Australian Mus., 2:105-106, 1896), the type and only species of the genus previously described.

Pugnus maesae, new species

Figure 1

Pugnus sp. Maes, 1967, p. 141, pl. 14, fig. D.

Description of holotype: Shell minute, solid, white, short-cylindrical, slightly broader posteriorly; surface polished; involute, spire immersed, covered by a pad of callus; aperture as long as shell, nearly straight, narrow, widening somewhat anteriorly, arching above summit of body whorl; outer lip varicose externally, thickened and denticulate within, the denticles very fine and close together on central portion of lip, larger and more widely spaced anteriorly and posteriorly; body whorl slightly contracted medially, sculptured with approximately 40 wavy spiral grooves which are crossed by very fine raised axial threads; parietal wall covered by thin, transparent, well-defined layer of smooth callus which bears a longitudinal row of about seven weak, irregularly spaced tubercles; anterior portion of columella having four evenly spaced, oblique folds (including fold at base of columella), most anterior fold the largest; folds decreasing in size and becoming more horizontal posteriorly; anterior margin of shell produced, evenly rounded, without a siphonal notch. Length 1.5 mm, breadth 1.1 mm.

Type locality: One mile north of Tanjong Puji, West Island, Cocos-Keeling Islands, Indian Ocean; dredged in 6 feet (1.83 m), coral mud and sand, with some *Caulerpa* algae; collected by R. Ostheimer and V. Orr (Maes), 30 January 1963.

Type material: Holotype, Academy of Natural

Sciences, Philadelphia, No. 288324. Eight paratypes, ANSP No. 32474, from same locality as holotype.

Referred material: ANSP No. 288311, one specimen, from two miles east of Ujong Tanjong, West Island, Cocos-Keeling Islands, in 4 fathoms (7.32 m), hard sand and weed; Ostheimer, Orr, Ross, collectors, 11 February 1963.

Discussion: From *Pugnus parvus* Hedley, originally described from Manly, near Sydney, New South Wales, the new species differs in several shell details: *P. maesae* has four nearly equal columellar folds; *P. parvus* has two large folds and a smaller, deeply seated fold posterior to them. *Pugnus maesae* has denticulation on the outer lip; *P. parvus* has none. The specimens of *P. parvus* examined by the author, from Mallacoota, Victoria (nearly 300 miles south of Sydney), were rather narrower, in proportion to their length, than the new species. They showed a curious surface sculpture of shallow hexagonal pits arranged "honeycomb" fashion, elongating behind the outer lip into spiral sculpture like that originally described



Figure 1. *Pugnus maesae*, new species. Ventral view of holotype. Copy, Maes, 1967, pl. 14, fig. D.

for the species by Hedley. These specimens also had perforate apices.

Familial placement of the genus *Pugnus* is uncertain. It was described by Hedley (1896) as a member of Ringiculidae, and Zilch (Handbuch der Paläozoologie, 6:1-835, 1959) placed it in Cephalaspidea. Maes (1967) transferred it to Marginellidae, remarking on its resemblance to the [marginellid] genus *Marginellopsis* Bavay, 1911. The character of the columellar folds and the lip denticulation appear typically marginellid. The wavy, incised spiral sculpture recalls that of some cephalaspidean genera, such as *Acteon* Montfort, 1810. Knowledge of its true relationships awaits an anatomical study.

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A NOTOPHYCID POLYCHAETE FROM CALIFORNIA

While collecting at a floating boat dock in Bodega Harbor, California, one of us (Belman) found a thick gelatinous sac attached to a colony of a hydroid (*Obelia* sp.). A polychaete was moving around inside the sac; this worm could not be identified as any polychaete reported from California (Hartman, Atlas of errantiate polychaetous annelids from California, Allan Hancock Foundation, Los Angeles, 1968; Atlas of the sedentariate polychaetous annelids from California, Allan Hancock Foundation, Los Angeles, 1969) and turned out to belong to the family Notophycidae, recently described from New Zealand (Knox and Cameron, Trans. Roy. Soc. New Zealand, Biol. Sci., 12:73-85, 1970). The Californian specimen differs from the other known specimens in several respects and is described as a new species in a new genus.

The relationship between the family Notophycidae and related polychaetes was discussed in detail by Knox and Cameron (1970).

Phyllodocella, new genus

Notophycids with a muscular proboscis, but without jaws.

The other known genus in the family, *Notophycus* Knox and Cameron (1970) has a pair of lateral jaws in the proboscis. Such jaws are absent in the present specimen.

The generic name refers to the resemblance between this notophycid and members of the Phyllodocidae.

Phyllodocella bodegae, new species

Figures 1 and 2

Material examined: Mason's Marina, Bodega Harbor, California, July 20, 1971, from a gelatinous sac attached to a colony of *Obelia* sp.; 15 cm depth on a floating boat dock; one specimen, Holotype deposited in the collections of the Allan Hancock Foundation.

Description: The holotype is a complete, sexually mature female with 24 segments that is 8 mm long and 2 mm wide without setae. It is white with reddish pigment spots over the anterior end in alcohol preservation.

The pygidium is a small, rounded cushion with out anal cirri; the anus is dorsal.

The prostomium (Fig. 1) is pentagonal and has two pairs of long, slender antennae near the anterior margin. A pair of small, distinct frontal lobes are present on the anteroventral margin. Two pairs of eyes are present at the middle and mid-posterior part of the prostomium; the anterior pair is lensed; the posterior pair is semi-lunular in shape. The peristomial segment is a complete ring, forming

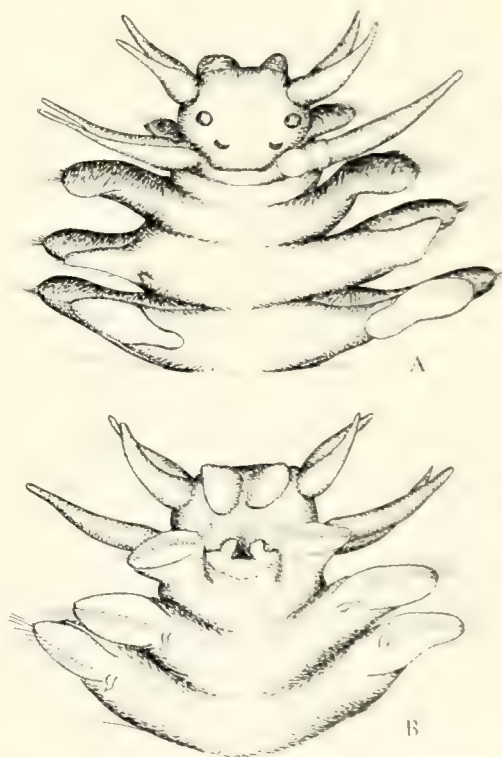


Figure 1. *Phyllodocella bodegae*, new species. A. anterior end, dorsal view, right dorsal cirrus broken. $\times 50$. B. anterior end, right dorsal view, right dorsal cirrus broken. $\times 50$.

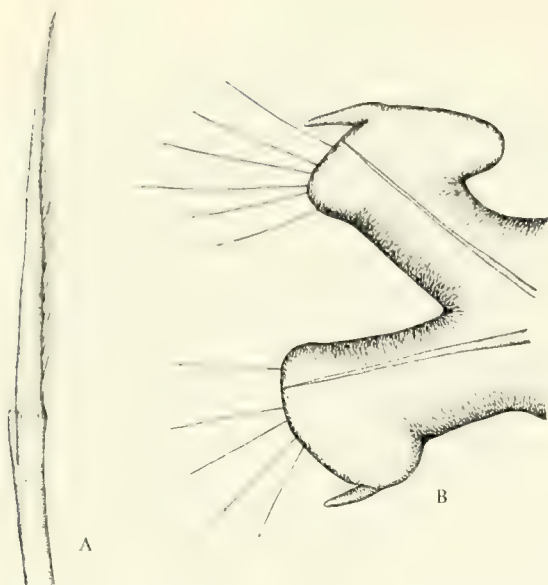


Figure 2. *Phyllodocella bodegae*, new species. A. seta from parapodium 7, $\times 950$. B. parapodium 7, anterior view, $\times 52$.

the lateral and posterior lips ventrally; it has two pairs of long, subdistally slightly inflated tentacular cirri.

The proboscis, which is strongly muscular, stretches through the four first setigers; jaws are absent.

Notopodia are absent in the first two setigers. The first neuropodia (Fig. 1B) project strongly ventrally with the setae pointing anteriorly and ventrally; the second neuropodia are slightly more lateral in position. Noto- and neuropodia project dorsolaterally and ventrolaterally in all setigers from setiger 3. Each parapodium (Fig. 2B), where fully developed, has similar, uni-acicular noto- and neuropodia. Each ramus has a cylindrical base and is distally expanded into a large, bulbous pad. The single fascicle of setae forms a straight line along the distal side of this pad. The notopodial pad is expanded to form a very large, bulbous lobe overhanging the dorsum in all setigers posterior to setiger 4; this development is absent in the two first pairs of notopodia. The dorsal cirrus is lateral to the notopodial bulbous lobe. The ventral cirrus, which is of the same size and shape as the dorsal one, is near the ventrolateral corner of the neuropodial pad.

All setae are composite spinigers. Each seta (Fig. 2D) has a long, slender shaft that is distally crenulated; it has a series of poorly defined transverse ridges subdistally. The appendage of each seta is long, evenly tapering and has series of fine teeth along the margin.

Discussion: *Phyllodocella bodegae* resembles *Noto-*

phycus minuta Knox and Cameron (1970) from Snares Island, New Zealand, in that it has two pairs of antennae and a single peristomial segment with two pairs of tentacular cirri and in the shape and structure of the parapodia. *Notophycus minuta* has a pair of lateral jaws in the proboscis; jaws are absent in *P. bodegae*. This character is here considered of generic rather than specific value. The two species further differ in the shape and detailed equipment of the parapodial lobes and in the development of the antennae and tentacular cirri.

Both species described in the Notophycidae are quite small and are probably easily overlooked by collectors; it is however, rather remarkable that these worms have not been seen more frequently, considering the apparent wide geographical distribution of the family.

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A KEY TO THE FISHES OF THE FAMILY GOBIIDAE (TELEOSTOMI) OF CALIFORNIA

Gobies comprise an interesting group of fishes, occupying diverse habitats along the Californian coast. They are frequently encountered in fish collections, yet a complete key to all species has never been published and identification, especially of preserved sub-adults, is often difficult.

All species are native to California except *Acanthogobius flavimanus* (Temminck and Schlegel) and *Tridentiger trigonocephalus* (Gill). Both of the above were introduced to the San Francisco area from the Orient. Listings for the occurrence of *Evermannia longipinnis* (Steindachner) in Californian waters are the result of an error by Fowler (1923), copied by Ulrey and Greely (1928) and Barnhart (1936) (Robert J. Lavenberg, pers. comm.) and thus this Gulf of California species is excluded from the key.

Several characters are taken from Jordan and Evermann (1896) and Norman (1957). Meristic counts that deviate from the above sources are the result of a study of the collections in the Natural History Museum of Los Angeles County and California State University, Long Beach, verified where possible by Clothier (1950).

FAMILY GOBIIDAE

Dorsal fins separate, the pelvic fins united to form a flaring cone-shaped sucking disc, free from the body (Fig. 1).



Figure 1.

1. a. Without five dark bands on leading edge of both the first and second dorsal fins; teeth in jaws simple, neither clubbed nor incised at their extremities (Fig. 2a) 2

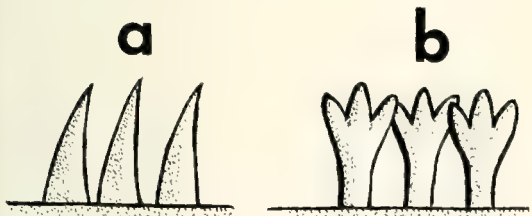


Figure 2.

- b. Five dark bands on leading edge of both the first and second dorsal fins (Fig. 3); outer



Figure 3.

row of teeth tricuspid, with
dilated. (Fig. 2b)
goby—*Tridentiger trigonocephalis* (C)



Figure 4.

2. a. Eyes normal; no specialized folds and flap in front and below the eyes 4
b. Eyes very small, vestigial or nearly so in the adults; cheeks much enlarged, tumid; skin of head with tactile organs well developed (Fig. 4) 3
3. a. Dorsal spines VI
Halfblind goby—*Lethops connectens* Hubbs.
b. Dorsal spines III Blind goby—*Typhlogobius californiensis* Steindachner.
4. a. Dorsal spines VII or less 5
b. Dorsal spines VIII Yellowfin goby—*Acanthogobius flavimanus* (Temminck and Schlegel).

5. a. Caudal fin normal, not greatly elongate; broad and rounded (Fig. 5a) 6

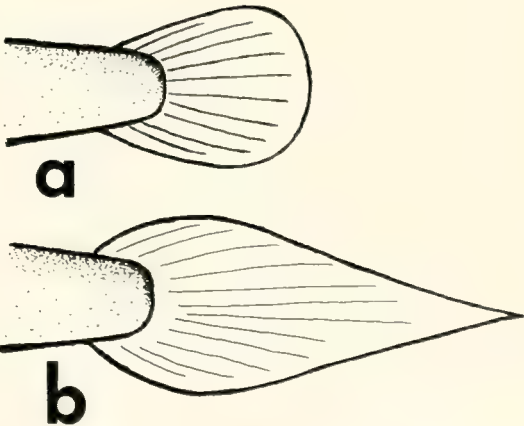


Figure 5.

- b. Caudal fin greatly elongate; pointed (Fig. 5b) Longtail goby—*Lus longicaudus* (Jenkins and ...)

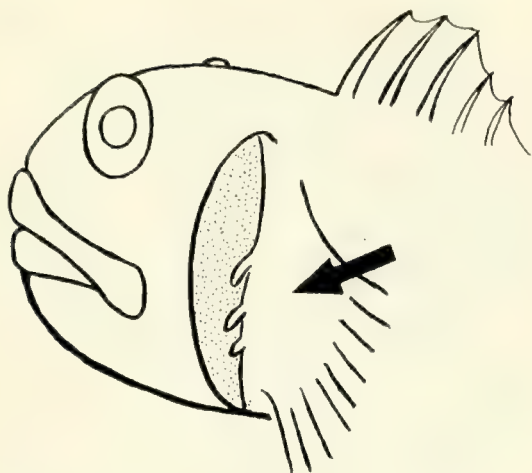


Figure 6.

6. a. Inner margin of shoulder girdle without dermal flaps 7
 b. Inner margin of shoulder girdle with 1 to 3 dermal flaps (Fig. 6) 11
7. a. Maxillary not extending beyond the posterior margin of orbit (Fig. 7a) 9
 b. Maxillary extending beyond the posterior margin of orbit (Fig. 7b) 8

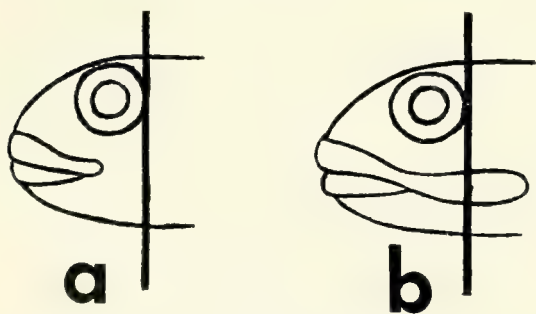


Figure 7.

8. a. Dorsal V to VI-I, 8 to 13; anal fin elements 9 to 14 Long-jaw mudsucker—*Gillichthys mirabilis* Cooper.
 b. Dorsal IV to V-O to I, 14 to 17; anal fin elements 15 to 18 Arrow goby—*Clevelandia ios* (Jordan and Gilbert).
9. a. Anal fin elements 13 or less 10
 b. Anal fin elements 14 or more Blue-banded goby—*Lythrypnus dalli* (Gilbert).
10. a. Anal I, 11(10 to 12); head and sides without crossbars encircling posterior part of

body Black-eye goby—*Coryphopterus nicholsi* (Bean).
 b. Anal I, 8(7 to 9); head and sides with 15 crossbars encircling posterior part of body
 Zebra goby—*Lythrypnus zebra* (Gilbert).

11. a. Anal fin elements 13 or more 12
 b. Anal fin elements 12 or less Tidewater goby—*Eucyclogobius newberryi* (Girard).
12. a. Maxillary not prolonged beyond the posterior margin of orbit 13
 b. Maxillary much prolonged beyond the posterior margin of orbit Shadow goby—*Quietula y-cauda* (Jenkins and Evermann).
13. a. Dorsal spines V; conspicuous blue-black metallic spot on opercle Cheekspot goby—*Ilypnus gilberti* (Eigenmann and Eigenmann).
 b. Dorsal spines VI or VII; no conspicuous blue-black metallic spot on opercle Bay goby—*Lepidogobius lepidus* (Girard).

COMMENT

Provisional species distributions given below were obtained from the card catalogues for fish collections at the Natural History Museum of Los Angeles County and California State University, Long Beach. Other sources included Barnhart (1936) and Clemens and Wilby (1961).

Tridentiger trigonocephalus.—Color variable. A distinctive black band followed by a pale yellow or white band encircling the base of the pectoral fins. Maxillary short not reaching to the middle of the eye. Habitat: sloughs and estuaries. Range: San Francisco Bay, California (L. Dempster, pers. comm.).

Lethops connectens.—Dorsal fins almost connected. Eye is functional in young, degenerate in adults. Specialized folds and flaps on head are apparent even in specimens less than 40 mm standard length. Habitat: tide pools. Range: Point Fermin to Carmel, California.

Typhlogobius californiensis.—Head covered with numerous folds and flaps. Eyes rudimentary in adults. Respiration almost entirely through pink-colored integument. Arrangement of free neuromast organs of the cephalic-lateralis system suggests that the Blind goby is not a simple derivative of the Half-blind goby. Adults live in pairs in the burrows of the Ghost shrimp *Callinassa affinis*. Habitat: rocky intertidal. Range: Cerros Island, Baja California to Point Vicente, California.

Acanthogobius flavimanus.—Color variable. Fourteen soft rays in dorsal fin with eight dusky spots, each somewhat larger than the eye-diameter, arranged in a nearly evenly-spaced series down each side, the first three being concealed beneath the pectoral fin; the last forming a more prominent spot at the base of the caudal fin (Brittan, Albrecht, and Hopkirk, 1963). Habitat: lagoons and estuaries ascending rivers to fresh water. Range: Elkhorn Slough to Tomales Bay, California (L. Dempster, pers. comm.). The range of this introduced species is expanding.

Gobionellus longicaudus.—Distinctive dark brown blotch on each shoulder above the origin of pectoral fin. A row of five dark blotches extending to the base of tail on both sides of body. Not closely related to other Californian gobies at least on the basis of the cephalic-lateralis system. Habitat: lagoons and estuaries. Range: San Diego Bay, California to Guayaquil, Ecuador.

Gillichthys mirabilis.—Maxillary extending posteriorly to base of pectorals in adult males. Capable of remaining alive out of water for several days, breathing aerially by means of heavily vascularized buccopharynx. Often found burrowed in the banks of mudflats at a level exposed by low tides. Habitat: channels of tidal mudflats and lagoons at the mouths of dry rivers. Range: Bahia Magdalena, Baja California to Tomales Bay, California; northern Gulf of California southward to Mulege on west side and Bahia Agiabampo on the east of Baja California (Barlow, 1961). Introduced into Salton Sea, California.

Clevelandia ios.—Capable of making rapid color changes to match varying substrates and light intensities. Black band on anal fin of mature males. During breeding season, both sexes develop yellow pigments on the ventral surfaces. At low tide or when threatened, Arrow gobies retreat to burrows of echinoid worms *Urechis caupo*, Ghost shrimp *Calinassa californiensis*, and Blue mud shrimp *Upogebia pugettensis*. Habitat: channels of tidal mudflats and estuaries. Range: Baja California to Vancouver Island, British Columbia.

Lythrypnus dalli.—First dorsal spines greatly extended. Colored orange-red with four to six dorsoventrally oriented blue bands. Lives in crevices on the sides or upper surfaces of reefs, frequently clinging to the rocks with its sucker. Habitat: reefs down to a depth of 100 m, commonly between 3 and 30 m. Range: northern Gulf of California; Cedros Island, Baja California to Morro Bay, California. I believe two specimens of this species, collected 10 November 1962 in Morro Bay and deposited in the fish collection of California State

University, Long Beach (C. S. L. B.), represent a northern range extension for the species.

Coryphopterus nicholsi.—Pale yellow or olive with a distinctive black margin on the first dorsal fin. Large black eyes. A fleshy crest on top of head extends posteriorly from behind eyes to origin of first dorsal fin. Habitat: commonly found between 5 and 50 m, resting on sand bottoms close to sand and rock interfaces; (it has been captured at depths greater than 700 m. This goby seldom venturing further than a few meters from protective cover). Range: San Martin Island, Baja California (Hibert and Turner, 1962) to the Queen Charlotte Islands, British Columbia.

Lythrypnus zebra.—Cherry red with 15 blue bars oriented dorsoventrally. Bars alternating with a thin blue line along the length of the body. Habitat: caves and under rocks or well within deep crevices; commonly found to depths of 30 m. Range: Cedros Island, Baja California to Ventura County, California.

Eucyclogobius newberryi.—Maxillary reaching to or slightly beyond the posterior margin of orbit. Olivaceous, with dorsals mottled. Live specimens quite transparent showing much of the internal organs. Habitat: shallow protected bays, estuaries, and clear freshwater streams which flow into the sea. Range: San Luis Obispo, Santa Barbara and Marin counties, California.

Quietula y-cauda.—The length of the maxillary increases with age and may not reach to posterior margin of orbit in specimens less than 30 mm standard length. Color variable. In young, black streak traversing dorsal portion of opercle at an angle, becoming indistinct in adults. Lower lip black. Black band on anal fin of mature males. A row of nine or ten dark blotches along the sides, the one at the base of the tail often shaped like the letter "Y". Enters burrows of invertebrates during low tide or when threatened. Habitat: channels of tidal mudflats. Range: Lower California to Morro Bay, California; northern Gulf of California, Baja California.

Ilypnus gilberti.—Maxillary extending to below middle of the eye. Conspicuous metallic blue-black spot on opercle. Habitat: shallow bays and channels of tidal mudflats. Range: northern Gulf of California; Bahia Magdalena, Baja California to Tomales Bay, California (L. Dempster, pers. comm.).

Lepidogobius lepidus.—Distinctive black on ventral surface of head and tips of all fins. Pale olive green, with rust colored blotches on sides. Muddy bottoms to 100 m depth. Range: Lower California to Vancouver Island.

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I wish to thank Camm Swift and Robert J. Lavenberg for their assistance and permission to examine the collections of the Natural History Museum of Los Angeles County, Dan Odenweller and Peter Haaker, California Department of Fish and Game, for obtaining data on the introduced Oriental gobies, and Lilian Dempster, California Academy of Sciences, San Francisco for distributional information and specimens of *Tridentiger trigenocephalus*.

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BULLETIN OF THE SOUTHERN CALIFORNIA
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ORNITHOPHILY AND EXTRAFLORAL COLOR PATTERNS IN *COLUMNNEA FLORIDA* MORTON (GESNERIACEAE)

C. EUGENE JONES, JR.¹ AND PAT VICKERS RICH²

ABSTRACT: Hummingbirds, such as the Little Hermit (*Phaethornis longuemareus*) and the Green-Crowned Brilliant (*Heliodoxa jacula*) apparently are attracted to the hidden flowers of *Columnnea florida* Morton (Gesneriaceae) by two conspicuous red spots located on the upper surface near the apex of the large leaves. This extrafloral attraction mechanism, in which the attracting unit, or leaf, does not simply simulate a portion of the flower, seems to be a new and unique type of hummingbird pollination system.

Most species of *Columnnea* (Gesneriaceae) possess a group of characteristics which tends to delineate ornithophilous plants (Morley, 1966; 1971). Although most hummingbird-pollinated species have bright red flowers, (Faegri and van der Pijl, 1966; Grant and Grant, 1968; Meeuse, 1961; Percival, 1965), some species of *Columnnea* lack prominent red flowers, and have small yellowish-orange blooms completely concealed by large leaves with red markings near the apices. We suggest that the red color patterns on the leaves serve as stimuli which increase the probability of visitation by hummingbirds.

Leaf and flower size, as well as flower color and the presence or absence of foliar color patterns, are quite variable in the genus *Columnnea*. The opposite leaves range from small (less than 1 cm long) and isophyllous to rather large (40 cm long) and anisophyllous. A detailed analysis of the nature of the extrafloral color patterns in the genus *Columnnea*, which is presently being completed, has revealed that, in general, species with small, isophyllous leaves tend to have large, conspicuous red flowers and no foliar pattern, whereas species with larger, anisophyllous leaves tend to have small yellowish-orange flowers concealed under the larger leaf. This leaf usually has a conspicuous red color pattern near its apex. The fact that flower size and color is related to leaf size and the presence or absence of red foliar patterns seems, in turn, to be directly associated with the mode of pollination.

One species with an unusual foliar pattern, *Columnnea florida* Morton, an understory, epiphyte, is conspicuous in the flora of the Premontane Wet Forest (Holdridge, 1967) of southeastern Costa Rica. The leaves of this species are strongly anisophyllous; the larger leaf may be 40 cm long and 11 cm wide, whereas the smaller is less than 1 cm long. The larger leaf completely conceals the relatively small (about 1½–2 cm long), yellowish-orange axillary flowers (Fig. 1a). A large blotch of red pigment is present on the lower (abaxial) surface near the apex of the leaf, but during most of the year the upper (adaxial) surface is a uniform dark green. Prior to the onset of flowering two conspicuous red spots (cover illustration) appear on the upper surface. Since *C. florida* is pollinated by hummingbirds, these spots may serve as flags advertising the concealed flowers to these birds.

METHODS

Field observations on hummingbird visitation of *C. florida* were conducted from 30 July to 1 August 1970, and from 31 January to 1 February 1972 at Finca Las Cruces, near San Vito, Puntarenas, Costa Rica. Visitations by pollinators were

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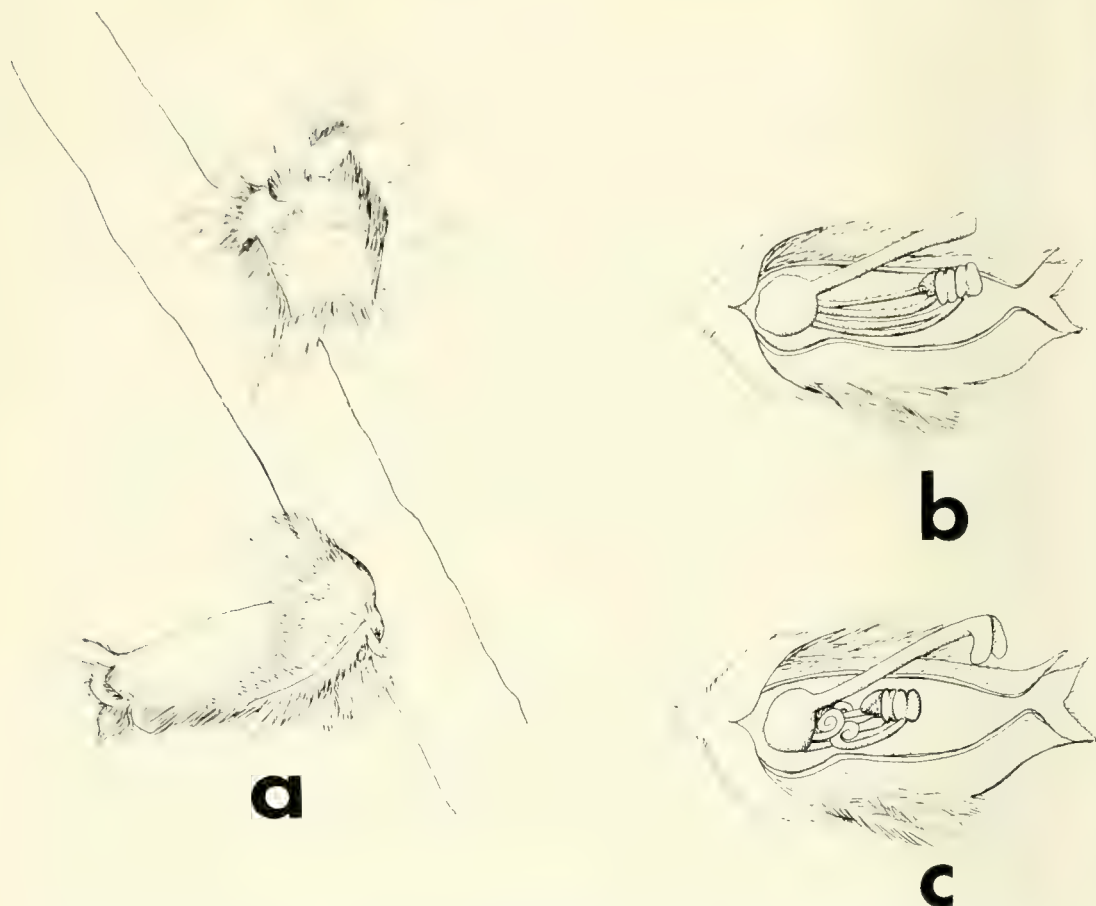


Figure 1. Flowers of *Columnnea florida* depicting front and side views (a) and lateral exposed views of the protandrous condition with the anthers extended and stigma closed (b) and the anthers withdrawn and stigma receptive (c).

observed primarily during the morning hours, from 0530 to 1200, since hummingbird activity was greatest during that time.

In 1970, a survey of *C. florida* in the area revealed that flowering had not begun. The plants chosen for observation were, therefore, somewhat modified to simulate natural morphological characteristics during the peak flowering period, as determined from the Flora of Costa Rica (Standley, 1937). On 30 July, two plants were selected and a pair of red spots, cut from orange-red surveyor's tape, was glued onto the leaves in the position where they normally appear. Yellow flowers from *Heliconia* sp. were trimmed to simulate the flower size of *C. florida* and inserted in the axils of the leaves. In 1972, observations were made on individuals of *C. florida* which were in bloom so modifications were unnecessary.

RESULTS AND DISCUSSION

During the observation period in 1970, only two species of hummingbirds, the Little Hermit (*Phaethornis longuemareus*—eight observations) and the Green-Crowned Brilliant (*Heliodoxa jacula*—four observations) visited *C. florida*. No other pollinators were noted on or near the flowers. Two behavioral patterns emerged when the birds spotted the conspicuous red pattern on the leaves. Two Little Hermits hovered directly above the two red spots and after 2–4 seconds dipped quickly under the large leaves and approached the axillary flowers. At this point the bill was inserted into the “dummy” flowers and the visitation completed. All other birds of both species followed a similar behavioral pattern but did not fly directly to the flowers. Instead these individuals appeared to discern the red cue, but did not perceive the

location of the food source. Consequently, these birds spent several seconds inspecting various portions of the plant before finding the flowers. It is our suggestion that the former hummingbirds were older birds, that had previously experienced this exceptional pollination system. The latter birds would then be younger, inexperienced individuals.

In 1970, actual visitations by these hummingbirds occurred only on 1 August 1970. Prior to that day 27 hummingbirds were observed in the immediate vicinity, but none actually visited the experimental plants. Perhaps, hummingbirds require some time interval before notice is made of signals regarding new food sources in the environment.

The Little Hermit (eight observations) was the only hummingbird seen visiting flowering plants of *C. florida* in 1972. The Little Hermit is a relatively small hummingbird, measuring only 3¼–4 inches from bill tip to tip of the tail. Its bill is slightly curved (Cover illustration) and varies from 2–2.5 cm in length as compared to the floral tube of *C. florida* which ranges from 2.5–3 cm long.

In the San Vito area of Costa Rica, *C. florida* flowers from late November until April (R. Wilson, pers. comm.). The flowers are protandrous. The dehiscing anthers are extended on elongated filaments positioned near the orifice of the corolla on the first day, followed the next day by a coiling of the stamen filaments removing the anthers and any remaining pollen from the opening of the flowers and from possible contact with visiting hummingbirds. Pollen is released into the wedge or "V" formed by the connation of the lateral axes of the four anthers. (Fig. 1b). Although the stigmatic surface also is positioned near the entrance of the flower, it is receptive only on the second day, thus decreasing the opportunity for self-pollination. When receptive, the stigmatic surfaces also form a "V" (Fig. 1c). The angle of the "V" formed by the connate anthers and the stigmatic surfaces is approximately the same as the angle of the upper bill of the Little Hermit. Upon insertion of the bill into the flower opening, pollen is deposited on the upper bill and transported from flower to flower in that way.

As Grant (1950) and Grant and Grant (1968) pointed out, flowers pollinated by hummingbirds usually have some means of ovule protection. In the case of *C. florida* it appears that the "V-shaped" nature of the connate anthers and the stigmatic surfaces serve to direct the bill away

from the superior ovary and into contact with the nectar which collects in a slight depression in the lower portion of the corolla. Since the flowers are horizontal to the ground, nectar collects in the depression in the corolla by gravity. An examination of 25 flowers from 10 separate plants, revealed no damage to the ovaries from the probing bills of the Little Hermit hummingbirds.

Behavioral responses of the Little Hermits were similar in 1972 to those noted in 1970, except six birds flew directly to the flowers of *C. florida* without first hovering above the red spots. This suggests that these hummingbirds may have had their feeding sites memorized and no longer relied on the extrafloral red spots as orientation cues. Thus, it would appear that the red spots on the leaves of *C. florida* are of prime importance as initial visual signals to hummingbirds denoting the presence of a new food source in the immediate area, but lose at least some of their importance as visual orientation cues after flowering begins.

Position and shape of the red spots on the leaf is of interest. Because this species is epiphytic on the trunks of large trees, the plants extend horizontally about 2 to 3 feet. As a result the most noticeable portion of the large nodding leaves is the upper surface near the tip, hence the location of visual cues there should be advantageous. Concentration of the red pigment into two distinct spots, rather than a single larger, red blotch, probably increases the effectiveness of the visual cue, since any consistently repeated pattern, associated with a food source, would be a more effective stimulus than randomly associated red blotches. The latter blotches would only provide a red flash, in the immediate environment, which might resemble those of other origins, and which would not predictably indicate the presence of a food source.

Our field observations of hummingbird behavior lead us to suggest that the red foliar spots are indeed functioning as visual cues, attracting hummingbirds, such as the Little Hermit and the Green-Crowned Brilliant, to the flowers of *C. florida*, thus insuring successful pollination. Although the attraction of hummingbirds to flowers by extrafloral mechanisms is well documented in the case of *Castilleja* and others, (Faegri and van der Pijl, 1966; Grant and Grant, 1968), the mechanism for *C. florida* is unique in that the leaf does not simulate a portion of the flower, but rather simply acts as a visual signal denoting the presence of nectar in the immediate vicinity.

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EFFECTS OF VARYING TEMPERATURES AND SALINITIES ON SETTLEMENT, GROWTH, AND REPRODUCTION OF THE WOOD-BORING PELECYPOD, *LYRODUS PEDICELLATUS*

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ABSTRACT: The larvae and adults of the wood-boring pelecypod, *Lyrodus pedicellatus*, were subjected to various conditions of temperature and reduced salinity under laboratory conditions. The effects of reduced salinity on the larvae were studied at 9-11 C, 14-16 C, and 22-24 C, and for the adults at 14-16 C and 22-24 C. Optimum activity for the larvae was found to be above 25‰ and from 14 to 24 C. The minimum temperature and salinity levels for larval boring were 12-14 C and 20‰. The long term minimum requirements for survival of adult *L. pedicellatus* was near 22-25‰ and about 11 C. Reproduction occurred above 28.8‰ in the temperature range of 14 to 24 C.

Lyrodus pedicellatus Quatrefages is one of three teredinids present on the Pacific Coast of North America. It is abundant in southern California and is reported north to San Francisco Bay (Miller, 1926). Many of the earlier reports referred to *L. pedicellatus* as *Teredo diegensis* (Turner, 1966). This species is frequently found associated with *Teredo navalis* and the colder

water shipworm, *Bankia setacea* Tryon. Both *L. pedicellatus* and *B. setacea* occur in Los Angeles-Long Beach Harbors with the former species the

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more prevalent (Menzies, Mohr, and Wakeman, 1963).

Little data are available on the tolerances of *L. pedicellatus* from the Pacific Coast. Barrows (1917) found this species able to temporarily withstand salinities as low as 10‰ in San Francisco Bay. Menzies *et al.* (1963) reported that larvae displayed maximal settlement during the warmer months of the year in Los Angeles-Long Beach Harbors. Roch (1940) determined that spawning occurred between 10 and 19 C, boring was reduced at 25‰ and death occurred below 20‰ in the Adriatic Sea. Edmonson (1942) found that the larvae were able to survive 10 days at 15‰ and adults survived 12 days in 17‰. Watson (1957) reported *L. pedicellatus* in Queensland, Australia only in salinities above 25‰.

Table 1 reviews the literature on temperature-salinity effects on teredinids. Species are arranged according to larval type (*i.e.*, oviparous, short or long-term larviparous). Oviparous forms are those that release their sex products directly into sea water where fertilization occurs; whereas, larviparous species undergo fertilization in the mantle cavity and brood the young to the straight hinge stage (short-term) or to the mature pediveliger (long-term), before releasing them (Turner, 1966).

The majority of the previous studies with *L. pedicellatus* have been based on field observations and have largely been based on short-term observations. The purpose of this study, therefore, was to define under laboratory conditions the temperature-salinity tolerances of the different stages, including settlement, growth, and reproduction, in the life cycle of this wood-boring pelecypod.

METHODS

Adult *Lyrodus pedicellatus* were obtained from small Douglas fir blocks which had been suspended from ropes at the surface to a depth of 3 m in the Cerritos Channel region of Alamitos Bay, Long Beach, California. The wood blocks were scraped free of fouling organisms bimonthly. The blocks were removed as required but generally they were suspended for about 6 months. Wood blocks were brought to the laboratory, placed in a gallon jar with aerated, filtered sea water, and placed in a cold bath at 14–16 C. To obtain larvae, the blocks were placed in a container with sea water at room temperature. This change in temperature generally caused the adult to release pediveliger larvae present in its brood chamber. The larvae were

pipetted from the container and the wood block were returned to the cold bath. The largest number of larvae were obtained by using the wood blocks the day they were removed from the field but they could be used as a further source of larvae in the future with decreasing success in obtaining large numbers.

Larval Salinity Experiments: An experiment was conducted to determine the effects of temperature and reduced salinity on the swimming, boring, and survival of the pediveliger stage. Eleven concentrations of sea water were used: 35.0, 31.5, 28.8, 25.2, 21.6, 18.0, 14.4, 10.8, 7.2, 3.6, and 1.8‰ salinity. Solutions were prepared by dilution with appropriate volumes of distilled water and the salinity determined (Barnes, 1959). A single 350 ml finger bowl containing a pre-soaked block of Douglas fir measuring 5 × 25 × 42 mm, was used at each salinity. Thirty swimming pediveligers were pipetted into each bowl and kept in reduced light at 22–24 C, 14–16 C, and 9–11 C. Cultures were examined every 6 hours and larval swimming, crawling, and boring activity including the formation of the calcareous cap was noted. The experiment was conducted for 10 days which was well beyond the potential period for larval boring.

Survival and Growth Experiments: The long-term effects of reduced concentrations of salinity on survival, growth, and reproduction in *L. pedicellatus* were conducted utilizing an experimental procedure similar to that described above. Individual swimming pediveligers were pipetted into petri dishes each containing a wood block and normal salinity sea water. Cultures were maintained at room temperature in reduced light. Larvae were allowed to bore for 14 days to allow sufficient time for the calcareous cap and siphons to become well developed. This experiment was designed to determine long-term salinity and temperature effects on adults. Eleven concentrations of sea water were prepared as before, namely, 35.0, 31.5, 28.8, 25.2, 21.6, 18.0, 14.4, 10.8, 7.2, 3.6, and 1.8‰ salinity. A wood block containing a single, healthy *L. pedicellatus* from the above cultures was placed in each of ten 500 ml stoppered erlenmeyer flasks with 100 ml of sea water at each salinity level. The experiment was conducted at 22–24 C and at 14–16 C giving a total of 110 specimens at each temperature. The 9–11 C temperature bath was unavailable for this experiment. Sea water in each flask was replaced by a fresh solution every five days. The experiment was terminated at five months at which time

TABLE 1. Review of literature on temperature and salinity effects on Tereidnids.

Oviparous Species	Larval Tereidnids			Adult Tereidnids			Locality	Source
	Optimum Activity	Minimum for Boring	Minimum for Survival	Optimum Activity	Minimum for Survival	Spawning		
<i>Bankia setacea</i>	—	—	—	above 20‰	—	—	San Francisco Bay	Kofoed, 1921
	—	—	—	—	7.5–13.7‰ lethal in 1–12 hr.	—	British Columbia (lab study)	White, 1929a
	—	—	—	—	—	above 15.8‰ in winter	British Columbia	White, 1929b
	—	—	—	reduced activity below 16‰	6.5‰ lethal in 24 hr.	—	San Francisco Bay	Miller, 1926
	—	—	—	—	—	7–12 C	Puget Sound	Johnson and Miller, 1935
	highest settlement at 9–23‰	—	—	—	—	—	British Columbia	Black and Elsey, 1948
	—	—	—	—	—	24–28‰ and below 10 C	Ladysmith Harbour, B. C.	Quayle, 1959
<i>Bankia gouldi</i>	raised to veliger in 16–40.4‰	—	no development below 14‰	—	—	—	British Columbia (lab study)	Townsley <i>et al.</i> , 1966
	—	—	—	common in 9–30‰	—	probably begins at 16–20 C	Chesapeake Bay	Scheltema and Truitt, 1954
	—	—	—	—	—	17.5–30 C	North Carolina (lab study)	Culliney, 1969
<i>Bankia bagidaensis</i> (= <i>bipennata</i>)	maximum settlement 3–12‰	—	—	—	—	—	Ivory Coast	Rancurel, 1971
<i>Bankia australis</i>	—	—	—	—	—	breeding peak about 20 C	New Zealand	Ralph and Hurley, 1952

TABLE 1. (Continued)

Oviparous Species	Larval Tereidinids			Adult Tereidinids			Locality	Source
	Optimum Activity	Minimum for Boring	Minimum for Survival	Optimum Activity	Minimum for Survival	Spawning		
<i>Bankia campanellata</i>	—	—	—	common in 21–34‰	—	—	Visakhapatnam Harbor, India	Nagabhushanam, 1961
<i>Bankia minima</i> (= <i>carinata</i>)	—	—	—	—	—	20–24 C	Adriatic (lab study)	Roch, 1940
<i>Teredo</i> (<i>Noto-teredo</i>) <i>norvagica</i>	—	—	10‰	—	—	—	Plymouth, England (lab study)	Harington, 1922
<i>Teredo utriculus</i> (= <i>Nototeredo norvagica</i>)	—	—	—	boring reduced at 29–31‰ below 10‰	28‰	20–30 C	Adriatic (lab study)	Roch, 1940
<i>Nausitora dunlopei</i>	—	—	—	—	—	below 10‰	Queensland, Australia	Watson, 1936; Smith, 1963
Short-Term Larviparous Species	Larval Tereidinids			Adult Tereidinids			Locality	Source
	Optimum Activity	Minimum for Boring	Minimum for Survival	Optimum Activity	Minimum for Survival	Spawning		
<i>Teredo navalis</i>	—	—	10–15‰	—	7.5–10‰	—	San Francisco Bay	Kofoid, 1921
	—	—	—	9‰ or above	6‰ lethal in long run	—	San Francisco Bay (lab study)	Blum, 1922
22.8 C optimal for development	—	—	7.5 C; below 7.5 or above 40‰	no boring below 10‰	—	—	Nova Scotia (lab study)	M'Gonigle, 1926
—	—	—	—	—	4‰ lethal in 4 days about 13 C	9‰ or above	San Francisco Bay	Miller, 1926
—	—	—	—	18 C and 21–30‰; no boring below 10‰	—	—	Atlantic Canada	Anon., 1927

TABLE 1. (Continued)

Short-Term Larviparous Species	Larval Tereidinids		Adult Tereidinids			Locality	Source
	Optimum Activity	Minimum for Boring	Minimum for Survival	Optimum Activity	Minimum for Survival	Spawning	
<i>Teredo navalis</i>	—	—	—	9% or above	5% in long run	—	Kofoed and Miller, 1927
	—	—	—	—	—	above 11 or 12 C	Grave, 1928
	—	—	—	growth down to 10 C and below	—	—	Needler and Needler, 1940
	—	—	—	—	—	11-24 C	Roch, 1940
20-30 C; swimming halted at 10-12 C	—	—	below 12 C; above 35 C	—	—	—	Bulatov, 1941
—	—	10%; below 14 C or above 26 C	—	—	—	18 C and above	Imai <i>et al.</i> , 1950
18-27 C; above 12% for development	—	—	below 10 C or above 30 C lethal	—	—	—	Kudinova- Pasternak, 1962
—	—	—	—	—	—	14 C or above; larvae released 16-20 C	Loosanoff and Davis, 1963
maximum settlement occurs 24-27 C	—	—	—	—	—	—	Ryabchikov and Nikolaeva, 1963

TABLE 1. (Continued)

Long-Term Larviparous Species	Larval Teredinids		Adult Teredinids		Locality	Source
	Optimum Activity	Minimum for Boring	Minimum for Survival	Optimum Activity	Minimum for Survival	Spawning
<i>Teredo poculifer</i>	—	—	—	—	common below 10‰	—
<i>Teredo furcillatus</i> (= <i>furcifera</i>)	normal swimming above 17‰	—	6‰	—	—	—
<i>Teredo bartschi</i>	—	—	survived 10 days at 15‰	—	survived 12 days in 17‰	—
<i>Lyrodus pedicellatus</i>	—	—	—	—	about 10‰	—
	—	—	—	boring reduced below 25‰	20‰	10-19 C
	—	—	survived 10 days in 15‰	—	survived 12 days in 17‰	—
	14-24 C; above 25‰	near 12-14 C; about 20‰	about 10 C; 20‰	above 25‰; 14-24 C	near 22-25‰; about 11 C	above 28.8 C; 14-24 C+
<i>Teredo tristi</i> (= <i>Lyrodus</i> <i>pedicellatus</i>)	—	—	—	—	not found below 25‰	—

Queensland,
Australia

Watson, 1957

India
(lab study)Nagabhush-
anam, 1963Hawaii
(lab study)

Edmonson, 1942

San Fran-
cisco Bay

Barrows, 1917

Adriatic
(lab study)

Roch, 1940

Hawaii
(lab study)

Edmonson, 1942

Long Beach,
Calif.
(lab study)

Present study

Queensland,
Australia

Watson, 1957

TABLE 2. A comparison of the survival of *Lyrodus pedicellatus* larvae and adults under reduced salinity conditions at the end of seven days at two temperature levels.

Salinity (%)	14-16°C		22-24°C	
	% Larval Survival*	% Adult Survival**	% Larval Survival*	% Adult Survival**
35.0	90	100	70	100
31.5	65	100	70	100
28.8	70	100	50	100
25.2	60	100	10	90
21.6	50	100	8	50
18.0	50	100	3	40
14.4	35	100	0	40
10.8	0	60	0	10
7.2	0	20	0	0
3.6	0	0	0	0
1.8	0	0	0	0

* Based upon 30 larvae tested at each salinity level.

** Based upon 10 adults tested at each salinity level.

all living animals were removed from their burrows. Measurements were made of the burrow and pallet length. The mantle cavity and gill filaments were examined for the presence of veligers which were counted if present.

RESULTS

The results of the larval and adult experiments of reduced salinity at the two temperatures are summarized in table 2. These data indicate that the adults are much more tolerant of reduced salinities than larvae and, furthermore, both stages are tolerant of reduced salinities at the lower experimental temperature. The seven-day median tolerance level (TL_m) values for larvae and adults were 28.2 and 21.6‰, respectively, at 22-24 C and 18.0 and approximately 9.9‰, respectively, at 14-16 C. Three-day TL_m values for larvae were approximately 9.4, 11.5, and 18.7‰ at 9-11, 14-16, and 22-24 C, respectively.

Swimming activity of the pediveligers was found to be related to temperature and salinity as shown in table 3. Larvae were found swimming 24 hours following their release from the adult in salinities of 35.0, 18.0, and 14.0‰ at the respective temperatures of 22-24 C, 14-16 C, and 9-11 C.

Early boring activity of the larvae was reduced with decreasing salinity but increased with an increase in temperature (Table 4). Initial penetration of larvae into wood blocks occurred at salinities of 18.0 and 25.2‰ at temperatures of 22-24

TABLE 3. The effects of temperature and reduced salinity on the larval swimming activity of *Lyrodus pedicellatus* 24 hours after release.

Salinity (%)	Number of Swimming Larvae*		
	9-11°C	14-16°C	22-24°C
35.0	6	6	3
31.5	9	3	0
28.8	21	9	0
25.2	18	3	0
21.6	15	15	0
18.0	6	3	0
14.4	3	0	0
10.8	0	0	0
7.2	0	0	0
3.6	0	0	0
1.8	0	0	0

* Based upon 30 larvae tested at each salinity level.

and 14-16 C, respectively. Penetration occurred only at normal salinity at 9-11 C. It should be noted, however, that although larvae were able to penetrate the surface of the wood, the formation of a protective calcareous cap over the opening, which occurs under normal conditions, occurred only in salinities down to 21.6 and 31.5‰ at temperatures of 22-24 and 14-16 C, respectively.

The relationship between reduced salinity and burrow and pallet lengths of animals raised over a five month period at 14-16 and 22-24 C is represented in table 5. As the salinity levels decreased, the rate of burrowing and pallet formation diminished. At any given salinity, the burrow or pallet length was greater at 22-24 than 14-16 C.

Some adult specimens raised in isolation from the pediveliger stage for a five month period contained larvae at the end of the experiment. These data were summarized earlier (Eckelbarger and Reish, 1972), but 40, 25, and 11 percent of the animals contained normal larvae at 35.0, 31.5, and 28.8‰ at 14-16 C; whereas, 30 and 20 percent contained larvae at 35.0 and 31.5‰ at 22-24 C. This was the first report of self-fertilization in the family Teredinidae.

DISCUSSION

Effects on larvae of Lyrodus pedicellatus: The effects of reduced salinity on the survival of the larvae of *L. pedicellatus* were greatly influenced by temperature. The mortality was considerably higher at all salinity levels as the temperature increased. While lethal limits for temperature were not investigated, the 9-24 C temperature range

TABLE 4. The effects of temperature and reduced salinity on the boring of *Lyrodus pedicellatus* larvae at the end of a 10-day period.

Salinity (‰)	Number of Boring Larvae*		
	9–11°C	14–16°C	22–24°C
35.0	2	9**	19**
31.5	0	13**	16**
28.8	0	8	2**
25.2	0	4	4**
21.6	0	0	3**
18.0	0	0	2
14.4	0	0	0
10.8	0	0	0
7.2	0	0	0
3.6	0	0	0
1.8	0	0	0
Total	2	34	46

* Based upon 30 larvae tested at each salinity level.

** Calcareous caps formed.

TABLE 5. The relationship of burrow and pallet length to reduced salinity in *Lyrodus pedicellatus* at two temperature levels.

Salinity (‰)	Number of Animals	Burrow Length (mm)		Pallet Length (mm)	
		Range	Mean	Range	Mean
14–16°C					
35.0	11	15–25	20.9	2.0–3.1	2.5
31.5	8	13–21	15.3	1.8–2.5	2.1
28.8	9	7–16	10.5	1.1–2.6	1.7
25.2	5	5–12	8.0	1.0–1.6	1.3
21.6	0	—	—	—	—
22–24°C					
35.0	10	15–40	24.6	2.0–4.5	2.7
31.5	10	16–30	23.4	2.0–3.9	2.5
28.8	8	8–26	20.0	1.3–2.8	2.3
25.2	4	9–12	10.3	1.5–1.8	1.6
21.6	1	—	5.0	—	1.0

used in the experiments is close to that encountered under local field conditions.

From the larval salinity experiments, the three-day TL_m values showed the limiting salinity levels to be approximately 9.4, 11.5, and 18.7‰ at 9–11, 14–16, and 22–24°C, respectively. Death occurred within a few hours at 7.2‰ and below at all temperature levels. The three-day TL_m values are representative of the normal salinity tolerances of larvae since the majority of *Lyrodus* larvae penetrate wood during this period. Thus, larvae of *Lyrodus* are quite tolerant of low salinities over a short period of time, especially during the critical first few days after release from the parent. Edmonson (1942) reported that larvae of *L. pedicellatus* from Hawaii were able to tolerate 15‰ for 10 days in the laboratory; a result consistent with ours. This was the only laboratory investigation of the effects of reduced salinity on this species reported until now.

The effects of temperature and reduced salinity on the activity of the larvae demonstrated that larvae were able to swim in lower salinities at reduced temperatures. Swimming ceased at exposure to 10.8‰ or below at all but the lowest temperature level. Reduced temperature also extended the swimming period from the normal 18 to 36 hours as reported by Horvath (1951), Isham and Tierney (1953), and Lebour (1946). No swimming activity was observed at any salinity level 24 hours after release from the parent at 22–24°C. Some larvae, however, continued swimming for five days in the higher salinities at 14–16°C.

Larvae were also found swimming 13 days after release in higher salinities at 9–11°C with a corresponding reduction in swimming period as the salinity decreased. A similar shortening of the larval swimming period in response to higher temperature was reported for *T. navalis* by Imai, Hatanaka, and Sato (1950). But Bulatov (1941) found 20–30°C the optimum temperature range for *T. navalis* with swimming ceasing at 10–12°C. It should be noted that although swimming activity in *L. pedicellatus* was found in this study to increase at lower temperatures, newly metamorphosed pediveligers in the crawling stages displayed very little activity compared to those at higher temperature levels.

Temperature and reduced salinity noticeably affected the boring of the larvae. Reduced temperature and salinity restricted boring while higher temperatures increased boring and enabled larvae to bore even under reduced salinity conditions. Boring occurred down to 18.0‰ at 22–24°C but did not occur below 35.0‰ at 9–11°C. The calcification of the mound covering the burrow entrance, however, occurred only in salinities down to 21.6 and 31.5‰ at 22–24 and 14–16°C, respectively. No caps were formed by boring larvae at 9–11°C. Larvae failing to secrete a protective cap died. It is apparent then that even though penetration of the substrate can be accomplished at 9–11°C and in the lower salinity levels at 14–16°C and 22–24°C, successful boring is more restricted. *Lyrodus* larvae are probably

able to penetrate wood and continue growth much below 14 C and below a salinity of 21.6‰ (Table 1). Imai *et al.* (1950) reported *T. navalis* capable of boring in brackish water at a salinity of 10‰ but were able to bore only between 14–26 C. Bulatov (1941) found 10 C or below lethal for the larvae of the same species. It would appear then that *L. pedicellatus* is as capable of boring under temperature conditions as low as *T. navalis* but is considerably more restricted by salinity conditions than the latter species.

The cold water species, *Bankia setacea*, is apparently more hardy than either *Teredo* or *Lyrodus* for it has been reported to bore in salinities of 9‰ at a temperature of 7 C (Trussell, 1967). Black and Elsey (1948) also found this species settling in greatest numbers when the surface salinity in British Columbia waters ranged from 9–23‰.

Salinity alone is probably not a significant factor for the survival of *Lyrodus* larvae in southern California since the salinity is seldom altered from that of normal sea water except directly following a heavy rain (Stone and Reish, 1965). These salinity changes are of short duration and usually restricted to surface waters. Since larval settlement generally increases with increase in water depth (Menzies *et al.*, 1963), the effects of these salinity changes in southern California are probably of minor importance. Temperature, however, does fluctuate throughout the year and appears to place significant limitations on boring activity. In this study, for example, the number of larvae boring decreased with decrease in temperature with a total of 46, 34, and 2 larvae boring at 22–24, 14–16, and 9–11 C, respectively. Reduced temperature also delayed the boring process. Boring began within 24 hours at 22–24 C but was delayed for 48 hours at 14–16 C and for five days at 9–11 C. These findings differ from those of Horvath (1951) who reported *L. pedicellatus* unable to bore 24 hours after release from the parent. Coe (1941) stated that boring in this species can occur up to two weeks after release but observations in this investigation have never shown boring to occur after such an extended period.

Settlement of *Lyrodus* larvae appears to be a year-round phenomenon in southern California waters although seasonal differences can be observed which probably reflect temperature fluctuations. Horvath (1951) indicated that *Lyrodus* larvae were released throughout the year in Los Angeles-Long Beach Harbors but that survival and development did not occur during the cold months of December through March. Menzies *et al.*

(1963) also indicated that in the same harbor, *Lyrodus* larvae settled during all seasons of the year with maximum intensity occurring during the warmer months of the year. The authors noted, however, that boring larvae failed to mature when temperatures reached a low of 12 C. Greenfield (1952) also reported *L. pedicellatus* actively breeding and boring throughout the year at Miami, Florida; an area approximating hydrographical conditions in southern California.

These field studies tend to agree with the findings of our laboratory investigation with heaviest settlement and boring occurring when temperatures reached 22–24 C. At the lowest temperatures tested, however, larval mortality was high, with few larvae successfully penetrating the substrate. Utilizing the temperature data of Moore and Reish (1969) in Alamitos Bay, California, the annual temperature ranged from about 13 to 24 C, with the warmer peaks occurring during the months of March through August. These data probably explain the maximum infestation observed during the period from April to September of wood blocks suspended bimonthly in this study, from August 1967 to February 1969.

Effects on adults of Lyrodus pedicellatus: Experiments on the effects of temperature and reduced salinity on the adults of *L. pedicellatus* disclosed that the adults were more tolerant to environmental stress than larvae. A comparison of the seven-day TL_m values at 22–24 C (Table 2) showed that larvae and adults displayed values of 28.8 and 21.6‰, respectively; whereas, these values dropped to 18.0 and 9.9‰, respectively, at 14–16 C. This greater salinity tolerance in adults is probably best explained on the basis of both physical protection from the environment and developmental stage. Animals used in the experiment had been boring for 14 days and all had formed caps and pallets. As is probably true in all shipworms, the sealing of their burrow entrances with their pallets provided an effective deterrent to osmotic stress.

White (1929b) discussed the protection afforded teredinids by their burrow and pallet mechanism. He found *Bankia setacea* less tolerant of reduced salinities when directly exposed to sea water than when in intact burrows with death occurring in one hour in 7.5‰ and within 12 hours in 13.7‰ at 15.5 to 19.5 C. Roch (1940) reported 25‰ the minimum salinity required for normal burrow activity and 20‰ lethal for *L. pedicellatus*.

During the course of the reduced salinity experiments with *Lyrodus*, disintegration of the pal-

lets and protective burrow caps occurred in specimens at low salinities. The formation of thinner shells and other calcareous structures in reduced salinities was reported in other molluscs by Newcombe and Kessler (1936). It is probable that the inability of *Lyrodus* to maintain these protective structures accelerated death due to the direct exposure of the animals to the external medium.

Temperature and salinity greatly affected growth in *L. pedicellatus* over a five month period. Total growth was determined by measuring the burrow and pallet lengths since neither varies with the spawning condition of the animal (Quayle, 1959). The average burrow lengths of experimental animals decreased with decrease in temperature and salinity. Reduced salinity presumably reduced growth by halting or slowing boring and feeding. Roch (1940) found 25‰ sufficient to reduce boring activity in *L. pedicellatus*. M'Gonigle (1926) reported no boring by *T. navalis* adults at 3.5‰ or below, and Blum (1922) observed that *T. navalis* did not produce fecal pellets at salinities of 4.0 to 5.0‰. Shipworm growth then is probably halted because the animal seals its burrow and remains relatively inactive until more favorable conditions return. Similarly, the bivalve *Mytilus edulis* remained closed and failed to produce byssal threads at reduced salinities (Reish and Ayres, 1968). It is also possible that under reduced salinity conditions the rate and efficiency of food metabolism is reduced as Kinne (1963) reported for *M. edulis*.

The effects of temperature on the growth rate of *L. pedicellatus* were readily apparent from this study with the average burrow lengths of animals raised at 22–24 C greater than those at the same salinity levels raised at 14–16 C. Isham, Smith, and Springer (1951), investigating *L. pedicellatus*, M'Gonigle (1926) and Needler and Needler (1940), both working with *T. navalis*, and Quayle (1959) studying *B. setacea*, all reported the maximum growth rate in the field corresponding to maximum seasonal temperature.

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TWO NEW SPECIES OF POLYCHAETOUS ANNELID WORMS FROM BAFFIN BAY AND THE DAVIS STRAIT

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ABSTRACT: Two new species of polychaeta of the families Lumbrineridae and Scalibregmidae from Baffin Bay and the Davis Strait are described. Both species occur in relatively deep water and were obtained by qualitative dredge hauls. A table emphasizing some taxonomic characteristics of some scalibregmid genera is presented.

During August 1968, the author participated on the shakedown cruise of the National Science Foundation's new polar research vessel, the R/V HERO to the waters of the Labrador Sea, Baffin Bay, and the Davis Strait. The present paper describes two new species of polychaeta in the families Lumbrineridae and Scalibregmidae. The type material is deposited in the United States National

Museum, Washington, D. C. Complete results of the cruise are being compiled and will be published in a subsequent paper.

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Family Lumbrineridae

Lumbrineris fauchaldi, new species

Figure 1

Material examined: Davis Strait (lat. 66° 29' N-long. 57° 26' W), HERO Station 28D, collected 17 August 1968, dredged in 580–610 m on a bottom of soft mud (7 specimens, TYPE).

Description: The material consists of 7 specimens, only one of which is complete (Holotype). The holotype is coiled, contains approximately 80 setigerous segments and measures about 10 mm in length. The longest anterior fragments measure 12 mm (44 setigers) and 15 mm (65 setigers) in length. The specimens are light tan in color with no body pigmentation.

The prostomium is conical and slightly longer than wide (Fig. 1a). There are no visible nuchal organs or eyes. The two peristomial segments are achaetous and similar in size. There are paired anterior prolongations of the first peristomial segment.

The body is rather slender, tapering at the posterior end and terminating in two anal cirri (Fig. 1b). One specimen had three anal cirri (Fig. 1c).

Setigers throughout are wider than long. The parapodia contain short rounded presetal and postsetal lobes. Setigers 1–10 contain fascicles of limbate setae. Thereafter, the dorsalmost setae in the fascicle exhibit blunted ends. These blunt setae grade into hooded hooks over succeeding setigers. The fully developed hooks do not occur until setigers 25–35. Some of the limbate setae of setigers 20–50 contain greatly enlon-

gated capillary tips (Fig. 1d). The hooded hooks completely replace the limbate setae in the last 1/3 of the body. Hooded hooks are multidentate with about 10 small teeth, of which the lowermost tooth is only slightly thicker than the rest (Fig. 1e). The acicula are yellow, straight, and may number two per parapodium in posterior setigers.

The pharyngeal apparatus is as follows (Fig. 1f): the maxillary carriers are short and sharply pointed, with a weak lateral notch; maxilla I has a weakly curved tip with no distinct teeth along the inner margin; each maxilla II has five teeth on the inner margin and a posteriorly directed lateral prolongation; each maxilla III and IV has one tooth; the mandibles were not observed.

Distribution: Davis Strait, depth ranging from 580–610 m.

Remarks: *Lumbrineris fauchaldi* belongs to species group II.b.1. (Fauchald, 1970), in which there are simple hooded hooks, which are multidentate in posterior setigers; maxilla III has one tooth. Approximately 35 species have been assigned to this group by Fauchald (1970). Of these, six are known to have limbate setae in median setigers with prolonged hair-like tips. Each of these species occurs in deep water. These species are *L. abyssorum* (McIntosh, 1885), *L. ehlersii tenuisetis* (McIntosh, 1885), *L. longensis* Hartman, 1960, *L. moorei* Hartman, 1942, *L. neozealandiae* (McIntosh, 1885), and *L. punctata* (McIntosh, 1885).

Lumbrineris abyssorum was described from 2,225 fathoms off western South America from fragmentary specimens in which the hooks had

TABLE 1. Some taxonomic characteristics of five genera of the Scalibregmidae having anterior acicular setae.

Genera	Branchiae	Parapodial Processes	Acicular Setae	Reference
<i>Asclerocheilus</i> Ashworth, 1901	Absent	Absent	Present in both rami of Setigers 1–3	Ashworth, 1901 Fauvel, 1927 Day, 1967
<i>Cryptosclerocheilus</i> new genus	Present Setigers 2–5	Absent	Limited to both rami of Setiger 2	This paper
<i>Parasclerocheilus</i> Fauvel, 1928	Present Setigers 2–7	Ventral cirrus on posterior setigers	Limited to notopodia of Setigers 1–4	Fauvel, 1928 Day, 1961
<i>Sclerobregma</i> Hartman, 1965	Absent	Dorsal and ventral cirri in posterior setigers	Limited to both rami of Setiger 1	Hartman, 1965
<i>Sclerocheilus</i> Grube, 1863	Absent	Ventral cirrus on posterior setigers	Present in both rami of Setigers 1–3	Ashworth, 1901 Fauvel, 1927

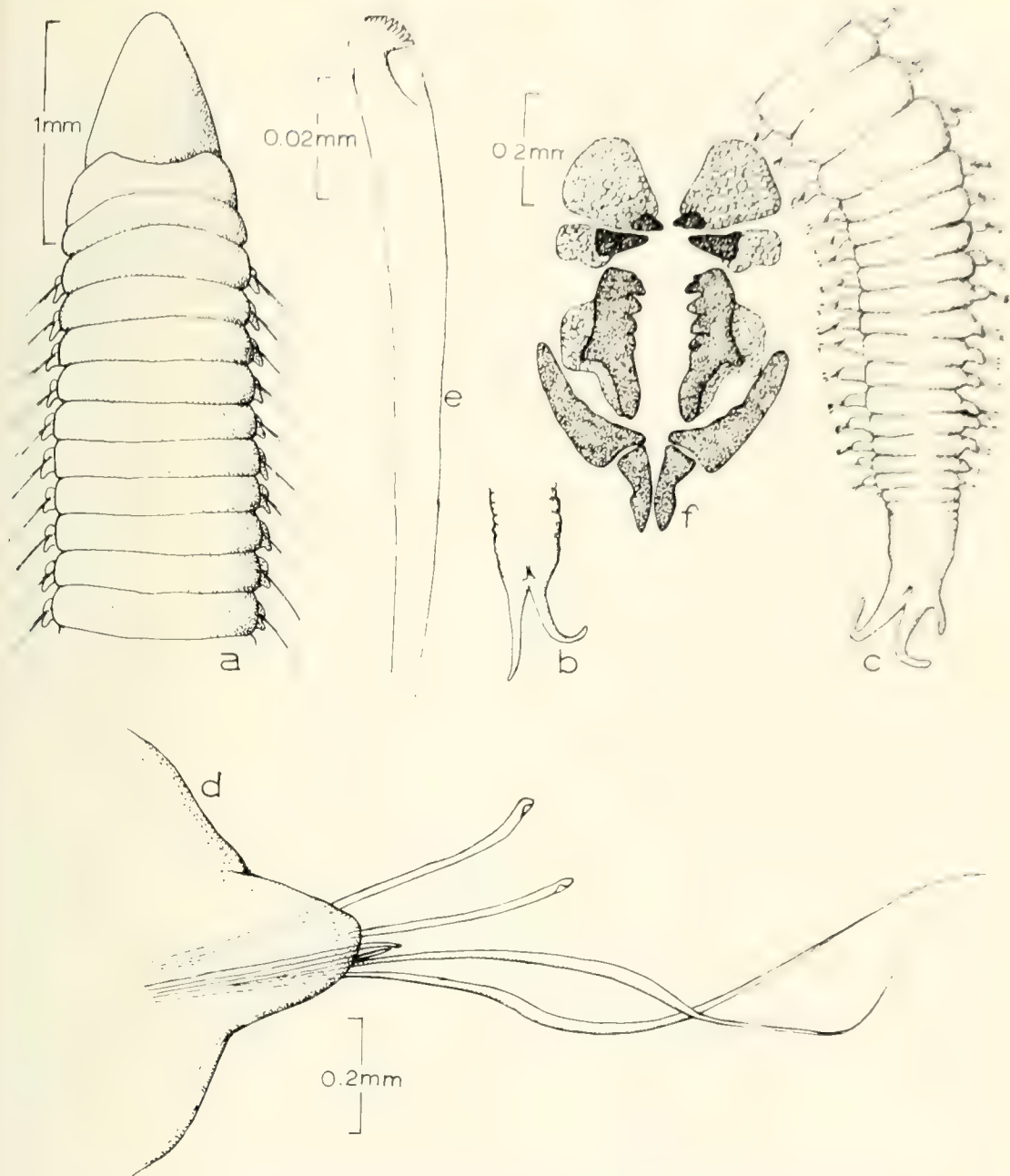
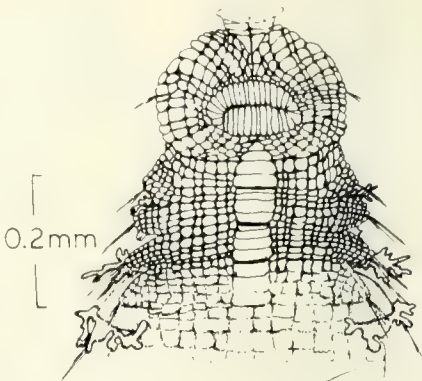
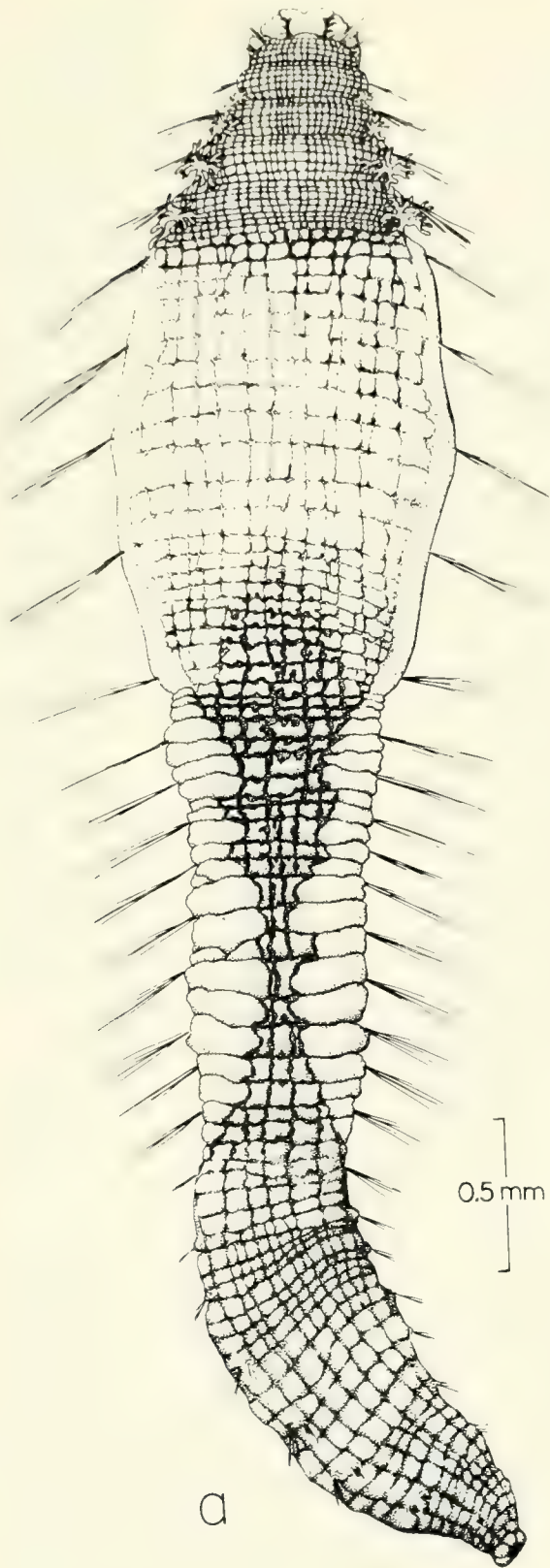


Figure 1. *Lumbrineris fauchaldi*, new species: a, anterior end in dorsal view; b, posterior end in dorsal view; c, posterior end in dorsal view; d, setiger 35 in anterior view; e, hooded hook from mid-body setiger; f, pharyngeal apparatus; a-c all to the same scale.

been lost or broken; *L. ehlersii tenuisetis* from off northeastern North America in 1,340 fathoms has five teeth on each side of maxilla II and two teeth on maxilla III; *L. longensis* has prolonged pre- and postsetal lobes in posterior setigers, in addition to black acicula; *L. moorei* has hooks from

approximately setiger 25, but there are no transitional setae as in *L. fauchaldi*; *L. neozealandiae* was apparently described from a group of species and type material needs to be reexamined; and *L. punctata* has only two teeth on the left side of maxilla II and three on the right.



It is a pleasure to name this species for Dr. Kristian Fauchald of the Allan Hancock Foundation, University of Southern California, in recognition of his monographic work on the superfamily Eunicidae.

Family Scalibregmidae

Cryptosclerocheilus, new genus

Type species: Cryptosclerocheilus baffinensis, new species.

Diagnosis: Body fusiform and elongated. Prostomium T-shaped, with two long frontal lobes. Without eyes. Peristomium achaetous. Proboscis unarmed. Branchiae limited to anterior segments. Parapodial lobes reduced to short elevations throughout the body; no cirriform processes present in either anterior or posterior regions. Lateral organs not evident. Acicular setae delicate and limited to setiger 2 where they occur in both the neuropodium and notopodium. Furcate setae begin on setiger 3 and continue on succeeding segments. Pygidium a simple lobed ring.

Remarks: *Cryptosclerocheilus* belongs to the group of genera having anterior acicular setae and a reduction in parapodial lobes and processes. The relationship of *Cryptosclerocheilus* with related genera is presented in table 1.

Cryptosclerocheilus baffinensis, new species

Figure 2

Material examined: Southern Baffin Bay (lat. 67°49' N—long. 60°46' W to lat. 67°38' N—long. 60°38' W), HERO Station 26, collected 16 August 1968, dredged in 1,830 m, on a bottom of brown sticky mud (4 specimens, TYPE).

Description: Length up to 55 mm, width up to 6 mm at the inflated portion. Segments number 24 to 30 in the four specimens available. The body is greatly inflated through segments 6 to 10. Thereafter it narrows to a slender abdominal region. The entire body is areolated and marked off with small rectangular raised areas (Fig. 2a). The parapodia are reduced throughout the body. There are no parapodial processes. The posterior end terminates in a simple lobed ring.

The prostomium is bifid with two prominent lobes (Fig. 2a, b). There are no eyes. The base of the prostomium is retracted into the achaetous buccal segment. The first setiger contains only capillary noto-

setae and neurosetae (Fig. 2c). The first setiger 2 are arranged in two tiers—the first tier consists of slender curved acicular setae (Fig. 2c) and a few furcate setae; the second group are long capillaries. The neurosetae have a similar arrangement, except that there are more of the acicular and furcate setae and fewer capillaries. The furcate setae completely replace the acicular setae on setiger 3. This arrangement of one bundle of capillary setae and another bundle of smaller furcate setae continues on succeeding setigers to the end of the body. The furcate setae have one tine longer than the other. Each tine is spinous along the inner border (Fig. 2d).

Distribution: Southern Baffin Bay, depth of 1,830 m.

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Figure 2. *Cryptosclerocheilus baffinensis*, new species: a, entire animal in dorsal view; b, anterior end in ventral view; c, capillary seta from anterior setiger; d, furcate seta from setiger 3; e, acicular seta from setiger 2.

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FLUCTUATIONS IN POPULATION DENSITY OF THE HISPID COTTON RAT: FACTORS INFLUENCING A "CRASH"

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ABSTRACT: A population of hispid cotton rats, *Sigmodon hispidus*, inhabiting a remnant grassland in west-central Kansas, near the northern limit of the range of the species, was live-trapped from April of 1965 through February of 1969. Until 1968, the population exhibited a pronounced annual cycle of abundance, varying from most abundant in autumn to least abundant in spring. Annual declines began at the time of normal cessation of breeding with the onset of winter, and were augmented by harsh winter weather. Monthly ecological densities ranged from 0.0-65.5 rats per hectare in the favored habitat. Population turnover was 92 percent complete in six months. In 1968, the population continued to exhibit a typical, seasonal pattern of fluctuation until autumn, but then underwent a "crash" that completely decimated the population. Biotic and environmental factors that might have influenced the crash included normal autumnal cessation of breeding coupled with predation, parasitism, and severe weather conditions. The balance between adverse winter weather and physiological and behavioral adaptations to survive suboptimal weather conditions probably is largely responsible for the location of the northern limit of the geographic range of *S. hispidus*.

During the course of ecological and physiological studies on cotton rats, *Sigmodon hispidus*, inhabiting a remnant grassland in west-central Kansas, we had the opportunity to monitor a "crash" in population density. Inasmuch as the population under study was near the northern limit of distribution of the species (Hall and Kelson, 1959: 673), we anticipated that analysis of factors that influenced the crash might reveal natural mechanisms that regulate northern dispersal of this immigrant Neotropical species. Therefore, the purposes of this paper are: 1) to present data on population dynamics of cotton rats at the latitude of Kansas; 2) to summarize factors that regulate annual fluctuations in population density of cotton rats; and 3) to relate those factors to the delicate balance between adaptation and environment that determines the location of the northern limit of distribution of the species.

METHODS

The 5.6-hectare remnant prairie in which the study was conducted is in the southeastern quarter of section 1, T. 14S, R. 19W, Ellis County, Kansas. The study area consists of six vegetative communities (Brock, 1968) that have remained relatively undisturbed in a climax condition for more than 60 years (Martin, 1960). Cotton rats were live-trapped, marked, and released during the first half of all but two months from April of 1965 through February of 1969. Both the study area and the procedures followed in gathering data were described in greater detail by Fleharty and

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Mares (1972). Determination of population densities was based on numbers of individual cotton rats caught during each trapping period. The paucity of previously uncaptured rats obtained at the close of each trapping period indicated that most rats on the grid had been accounted for (see Davenport, 1964; cf. Van Vleck, 1968). Ecological density (number per preferred habitat—Odum, 1971) was estimated by assuming that the population was distributed throughout the different habitats in the proportions shown by trap success (see Fleharty and Mares, 1972). From October of 1967 through February of 1969, weights of rats were recorded at the time of capture and the "capture calendar" method (Andrzejewski, 1963, 1967) was used to determine age structure of the population. Meteorological data were obtained from the Fort Hays Agricultural Experiment Station, which is located about two miles from the study area.

RESULTS

If data pertaining to the last year of study are disregarded, crude density (number per entire study area) ranged from a low of 0.2 per hectare (one rat on grid) in May of 1965 to a high of 20.6 per hectare (115 rats on grid) in October of 1967. Greatest densities occurred in autumn of each year, whereas least densities occurred in the springs of 1965, 1966, and 1968, and in summer of 1967 (Fig. 1). Males were significantly more numerous than females ($P < .05$); a total of 516 males (57 percent) and 390 females (43 percent) were captured.

Ecological densities were greatest in low-lying plant communities dominated by *Andropogon gerardi* (Fleharty and Mares, 1972). Monthly estimates of density in a draw, where the vegetation consisted principally of *A. gerardi*, *Kochia scoparia*, and *Helianthus annuus*, reached a peak of about 45.5 cotton rats per hectare in three of the four autumns, thus suggesting that the carrying capacity of this habitat was attained almost every year. The greatest ecological density recorded during the 47 months of trapping was 65.5 per hectare in October of 1966.

Rate of turnover of the population averaged 66 percent during the month following first capture, and turnover was 92 percent complete by the end of the sixth month. These figures do not differ appreciably from those reported by Odum (1955) and Goertz (1964). Average time spent on the study area was 52.1 days for males and 54.3 for

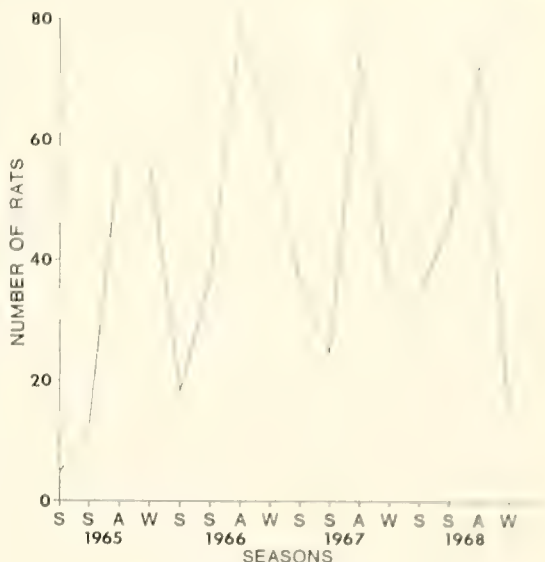


Figure 1. Line graph showing number of cotton rats caught on grid in spring, summer, autumn, and winter of 1965-1968.

females; however, these times are minimal estimates because no means of determining precise dates of natality and mortality were used. Two males were on the study area for at least 336 and 335 days, respectively, and one female survived at least 363 days. Goertz (1964) mentioned a male that survived for at least 12 months and a female that survived at least nine months.

Age structure of the population during a 15-month period suggests that most reproduction occurred during summer and autumn (Fig. 2). Juveniles were most numerous in autumn, and adults became most numerous in late winter when the surviving juveniles attained the weight (60 g) at which they were considered mature. Old adults were most numerous in summer, when the surviving adults attained the weight (110 g) that has been used to delimit the old adult age class (see Fleharty and Choate, 1972).

In November of 1968, when the population began its annual decline in density, the only notable difference in age structure as compared with November of 1967 was the fact that fewer than half as many old adults were present in the population (Fig. 2). By December of 1968, no old adults remained and the population contained only about half as many rats as it had during December of 1967. In January of 1969, only 16 cotton rats were caught on the study area, as compared with 86 only three months previously, and 12 of these

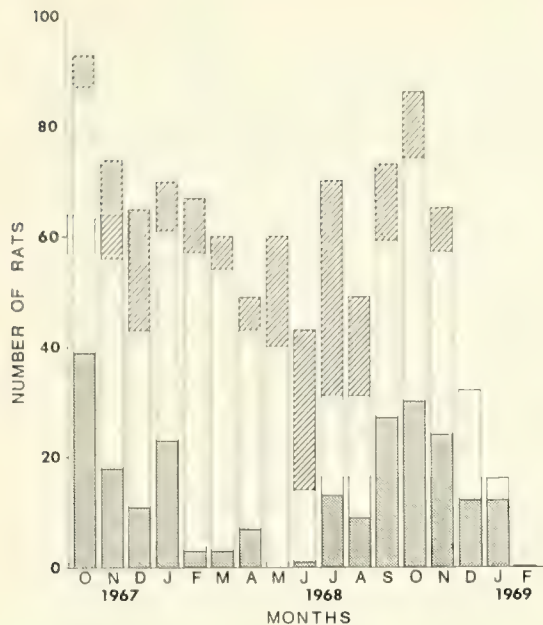


Figure 2. Age structure of population of cotton rats from October of 1967 through February of 1969. Diagonal lines represent old adults; plain represents adults; and stippled area represents juveniles.

were juveniles. No cotton rats remained on the study area in February of 1969, and subsequent snaptrapping in and around the remnant grassland resulted in no captures during March, April, or May of 1969.

DISCUSSION

Annual cycles of abundance, with greatest densities occurring in autumn and least densities in spring, were described for cotton rats by Komarek (1937), Odum (1955), and Provo (1962). Other authors (*e.g.*, Schendel, 1940; Cockrum, 1952; Fitch, 1958; Goertz, 1964; Hoffmann and Jones, 1970) have commented on the marked reduction in numbers of cotton rats that takes place between autumn and spring and have postulated that various aspects of winter weather might be responsible for population declines. However, our data indicate that annual population declines began in November, when there were few days in which the maximum temperature failed to exceed 0°C. It seems likely, therefore, that severe weather during late winter might act to accelerate an already declining population, but that biotic factors such as predation (see especially Schnell, 1968) and

the normal cessation of breeding interact in autumn to initiate the annual reduction in numbers.

At the latitude of Kansas, cotton rats reproduce mainly in summer and autumn (Bancroft, 1969); most breeding on the study area took place during the period June through October although, when data from all 47 months of the study were pooled, a few rats were trapped in reproductive condition in every month of the year (Fleharty, unpublished data). Coincident with decreased breeding, the number of juveniles that entered the population declined sharply in late winter and spring (Fig. 2). Therefore, animals lost from the population in late winter, for whatever reason, were not replaced.

A substantial percentage of cotton rats lost from the population in autumn and early winter likely were removed by predators. Schnell (1968) regarded a density of about 37 cotton rats per hectare as the "predator-limited" capacity for the species. With one exception in this study, density of cotton rats exceeded 37 per hectare in preferred habitats only in autumn and early winter, just before the advent of population declines. During these periods of high density, when the carrying capacity of preferred habitats probably was exceeded, rats moved out into less favorable habitats with reduced overstory (Fleharty and Mares, 1972) and undoubtedly were thereby subjected to increased predation by raptors. Sealander and Walker (1956) reported that cats, coachwhip snakes, and red-tailed hawks prey on cotton rats, and Schnell (1968) presented evidence in support of Odum's (1947) observation that the marsh hawk is a primary predator on cotton rats. Although we lack actual data on predation, marsh hawks were especially numerous over the study area in late autumn of each year (Ely, 1971), and likely fed largely on cotton rats during their peak period of abundance. Also, long-tailed weasels, snakes, and other predators were known to inhabit the study area, and probably preyed regularly on cotton rats, especially during their peak of abundance.

Acting together, predation (and other forms of mortality) and cessation of reproduction would be sufficient to initiate annual declines in abundance. However, severe winter weather undoubtedly augments those declines. The behavior of cotton rats in winter reflects their recent arrival from a region where the severity of winter weather is less than that which they experience today near the northern limit of their range. Cotton rats are not known to store food (Schendel, 1940), and periods of extreme cold effectively restrict foraging.

ing behavior (Goertz, 1964) and induce "huddling" (e.g., Schendel, 1940; Dunaway and Kaye, 1961; Wiegert and Mayenschein, 1966). Inactivity during cold weather thus would force cotton rats to expend their reserves of energy to maintain their body temperature, and might lead to "cold weather starvation" (Howard, 1951) during protracted periods of severe weather.

If cessation of reproductive activity, coupled with predation and other forms of mortality and augmented by starvation during severe winter weather, are responsible for annual declines in abundance of cotton rats, then the crux of the problem has to do with the factor or factors that acted with different intensity on the population to produce the crash in 1968–1969. Two factors that could have been involved are disease and parasitism. Stoddard (1931) and Davis (1958) both suggested that disease is an important cause of periodic population declines in cotton rats. Certainly, the high densities that are attained during autumnal peaks in density would be conducive to rapid spread of disease, but we have no evidence that disease was involved. However, we do have at least indirect evidence for a high incidence of parasitism. In conjunction with other research, it was noted that numerous cotton rats, especially old adults and adults, collected on and around the study area contained large numbers of nematodes—in some instances the stomachs were distended. Furthermore, if parasitism were involved in the population decline this might account for the fact that old adults were the first to exhibit a marked decrease in numbers (Fig. 2). Whatever the case, few cotton rats remained on the study area in December of 1968 when the effects of winter weather came to bear on the population.

Goertz (1964) discussed the effects of severe winter weather on a population of cotton rats in Oklahoma. He concluded (p. 376) that a "long period [11 days] of below-freezing weather, with snow on the ground and ground frozen . . ." contributed to a marked decline in population density of cotton rats. However, our data do not indicate what specific characteristic of winter weather was responsible for decimation of the population reported herein. In December of 1965, 57 cotton rats were present on the study area. No decline in numbers occurred during January and February of 1966 even though those months were considerably colder than normal; the average maximum temperature for the last 14 days of January and the first three days of February was less than -6°C , and 8–10 centimeters of snow covered the

ground for 16 days during this period. In December of 1966, 73 cotton rats were present on the study area, but by February of 1967 the population had declined to only 48 rats. The average maximum temperature for the last nine days of December was about -6°C , and a 15-centimeter snow cover was present. Some of this snow remained on the ground for the first 12 days of January. In December of 1967, 33 cotton rats were present on the study area. No decline in numbers occurred during January or February of 1968 although temperatures averaged slightly below normal. In December of 1968, 30 cotton rats were present on the area, but by February of 1969 none remained. Temperatures during December were the lowest recorded for that month since 1963; the average maximum temperature for the last 11 days was -5°C , and at no time during that period did the maximum temperature exceed 0°C . Also, eight centimeters of snow blanketed the ground for the last 13 days of December. The average maximum temperature for the first day and the last nine days of January of 1969 averaged well below freezing, and three centimeters of snow covered the ground for the first five days of the month. Even so, the weather conditions (at least so far as temperature and snow cover are concerned) were no more severe in the winter of 1968–1969 than they were in 1965–1966.

These data indicate that decimation of the population of cotton rats during the winter of 1968–1969 probably did not result entirely from weather conditions. If a cause-and-effect relationship were involved, then the population inhabiting the area during the winter of 1965–1966 seemingly would have experienced a crash like that which occurred three years later unless, for some reason, the rats inhabiting the area during the winter of 1965–1966 had more energy reserves to draw from than did the rats inhabiting the area during the winter of 1968–1969.

In an attempt to estimate the extent and utility of energy reserves in overwintering populations of cotton rats, we performed the following computations on the population that succumbed in the "crash" of 1968–1969. Energy contained within the population in January of 1969 was distributed among only 12 juveniles and four adults (mean weights, 56 and 78 grams, respectively). The body weight of juveniles consisted of 7.56 percent lipid, whereas that of adults consisted of 10.72 percent lipid (Fleharty *et al.*, 1972). If we assume that all but three percent of the lipid content was available for respiration as energy (Kleiber, 1961),

that the lipid released 9.093 kcal/g (Fleharty *et al.*, 1972) when respired, then lipid reserves of juveniles and adults amounted to 37.28 and 73.74 kcal, respectively. If the average dry weight of full stomachs is 1.04 in juveniles and 1.56 in adults (Fleharty, unpublished data) the assimilation efficiency of stomach contents is 88 percent (Davis and Golley, 1963), and the caloric content of the food eaten is 4.55 kcal/g (Fleharty, unpublished data), then the reserve energy of full stomachs is 4.14 kcal in juveniles and 8.11 in adults. These values added to caloric values of lipids yield totals of 41.43 and 81.85 kcal available to juveniles and adults, respectively, if severe weather resulted in a cessation of foraging. These figures might be increased somewhat if cotton rats resorted to feeding on dead nest mates (Schendel, 1949) or to cannibalism.

Pearson (1960) and Górecki (1969) noted the importance of "huddling" in reducing the rate of metabolism; however, the metabolic rate of huddling cotton rats remains unknown. In order to bracket the actual metabolic rate of huddling rats (which undoubtedly are exposed to microclimatic conditions less severe than those above the vegetation), the rates (Gaertner, 1968) at 0°C (3.20 cc O₂/g/hr) and at 32°C (1.26 cc O₂/g/hr) were used to compute the lengths of time that juveniles and adults could survive if totally dependent on stored energy. Assuming an oxy-caloric coefficient of 4.82 calories for both juveniles and adults, juveniles could survive using metabolic reserves for no more than 2.5 days at 0°C and only 5.1 days at 32°C; adults could exist on metabolic reserves for no more than 2.8 days at 0°C and only 8.1 days at 32°C. The actual length of time huddling rats could survive under field conditions doubtlessly falls somewhere between these two extremes. It should be pointed out, also, that as density decreased during the crash the huddling phenomenon to withstand cold would become less effective because it would be increasingly difficult to locate other rats.

Our calculations regarding length of survival of cotton rats when dependent strictly on energy reserves illustrate an important point. Huddling rats must make occasional forays in search of food or they could not survive even a relatively moderate winter near the northern limit of their distribution. Such forays, of course, increase the probability of predation, but the selective advantage resulting from replenishment of energy stores undoubtedly outweighs the effects of removal by predators of a few individuals from the popula-

tion, at least when the population is not already depleted by other factors. In any case, if we assume that winter weather was at least indirectly responsible for decimation of the population in 1969, then it is reasonable to suggest that energy reserves and huddling simply were not sufficient to enable survival of any of the cotton rats that remained on the study area during that winter period.

Therefore, it seems likely that predation and/or other forms of mortality, coupled with the normal cessation of reproductive activity, was responsible for initiation of annual declines in density of cotton rats, whereas winter weather acted primarily to accelerate declines by causing starvation of animals that lacked sufficient energy reserves to withstand periods in which foraging was restricted. Severe weather undoubtedly was at least indirectly responsible for final decimation of the population during the crash, but the effects of protracted cold might not have been so devastating if old adults and more adults had been present or if the remaining adults had not already been deprived of some of their energy reserves, perhaps by parasitic infection.

An alternative explanation for the crash is that it merely represented the depression phase of cyclic oscillation in population density. The possibility that populations of cotton rats exhibit periodic cycles of abundance was first suggested by Stoddard (1931). Komarek (1937) reviewed data on population fluctuations of cotton rats in the southern and southeastern United States, and concluded that this species undergoes regular cycles of abundance with a periodicity of four-five years. Observations of several other workers, on the other hand, would seem to indicate that oscillations in population density of cotton rats have a periodicity of about 10 years. Pronounced declines in population density of cotton rats were recorded in Oklahoma during the winter of 1939-1940 (Schendel, 1940); in Kansas during the winter of 1948-1949 (Cockrum, 1952); in Kansas during the winter of 1957-1958 (Martin, 1960); and in Oklahoma (Goertz, 1964), Tennessee (Dunaway and Kaye, 1961), and Texas (Haines, 1963) during the winter of 1959-1960. The crash of 1968-1969 reported herein occurred approximately when it would have been expected if *S. hispidus* undergoes cyclic oscillations in density with a periodicity of 9-11 years, but the low points shown in figure 1 might also be interpreted to indicate a periodicity of four years. We regard existing data on periodic cycles of *S. hispidus* as

inconclusive, but admit that regularly-expressed intrinsic factors might have prompted the crash observed in 1968–1969.

Whether the crash was a manifestation of cyclic intrinsic mechanisms or was caused by predation, disease, parasitism, or one or more of these combined with “cold weather starvation,” the delicate balance between weather conditions and energy (lipid) reserves undoubtedly is an important factor in determining the success of populations of cotton rats near the northern limit of their distribution (see Fleharty *et al.*, 1972), and likely is the single most important factor in determining the location of the northern limit of the range of the species. Northward dispersal of cotton rats in Recent time reflects a gradual increase in temperature that accompanied the last glacial retreat, but northward movement during the last century (Cockrum, 1948; Genoways and Schlitter, 1966; Hoffmann and Jones, 1970) has proceeded at a more rapid rate than is explicable on climatic grounds alone. It seems likely that this rapid northward dispersal has resulted in part from adaptations (Fleharty *et al.*, 1972; Fleharty and Choate, 1972) by cotton rats to facilitate survival in increasingly severe winter weather through stockpiling of energy reserves in the form of lipids that can be drawn upon during periods of limited activity.

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THE CORAL SNAKE *MICRURUS NIGROCINCTUS*
IN HONDURAS (SERPENTES: ELAPIDAE)

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ABSTRACT: Analysis of seven characters of scutellation and coloration of material of *Micrurus nigrocinctus* from Honduras indicates that variation in these characters is more complex than has formerly been recognized. The characters studied exhibit discordant patterns of variation but populations of *M. nigrocinctus* from northern Honduras are generally distinct from those from southern Honduras in a number of features. Populations from intermediate areas exhibit discordant admixtures of these characters. We suggest that application of names to infraspecific taxa in Honduras tends to obfuscate rather than illuminate variational trends in this coral snake.

Roze (1967, 1970) interpreted the variation in color pattern and scutellation exhibited by specimens of the coral snake *Micrurus nigrocinctus* (Girard) from Honduras as indicating the presence of two geographic races within that country. One subspecies, *M. n. divaricatus* (Hallowell), was envisioned as inhabiting northern and central Honduras, extending as far north as British Honduras. The other subspecies, *M. n. zunilensis* Schmidt, was considered to range along the Pacific slopes of southern Honduras, extending north to Chiapas, México. *Micrurus n. divaricatus* was characterized as having light bands present, 11 to 26 (usually more than 19) black body bands, and the black pigment of the red bands irregularly distributed (Schmidt, 1933; Roze, 1970). *Micrurus n. zunilensis* was characterized as having the yellow bands variable in length (0 to 2 scale rows long), 12 to 26 (usually less than 19) black body bands, and with very little or no black pigment on the red bands (Schmidt, 1933; Roze, 1970).

During examination of material of this species of coral snake from Honduras in preparation for a report on the snakes of that country, it became apparent that color pattern variation was much more complex than had formerly been recognized and that the taxonomic arrangement discussed above could not be accepted in its entirety. It is the purpose of this paper to discuss color pattern and scutellational variation of *Micrurus nigrocinctus* in Honduras and to suggest that the recognition of two subspecies in Honduras obfuscates, rather than elucidates the variational picture.

Eighty-four specimens of *Micrurus nigrocinctus* are available from widely scattered areas in Honduras. Unfortunately, most of these snakes were collected at a few localities, as about 80 percent

of the known specimens are from 4 of the 11 populations characterized below.

For the purpose of discussion of variation in color pattern and scutellation, we segregated the material into 11 samples (Fig. 1). Samples were set up utilizing specimens from geographically and altitudinally restricted areas with a more or less uniform vegetational cover. These samples, termed populations from this point on, may be characterized as follows.

Population A (23 specimens).—From localities in the Sula Plain at elevations from about 20 to 100 m in mixed scrub forest (Tropical Dry Forest formation of Holdridge, 1962).

Population B (24 specimens).—From localities in the western portion of the Nombre de Dios Piedmont at elevations from sea level to 30 m in tropical lowland rainforest (Tropical Moist Forest formation of Holdridge, 1962).

Population C (13 specimens).—From localities in the Sierra de Sulaco and nearby ranges at elevations from 1200 to 1300 m in disturbed or undisturbed broadleaf evergreen forest (Subtropical Wet Forest formation of Holdridge, 1962).

Population D (2 specimens).—From localities in the eastern portion of the Nombre de Dios Piedmont and the Sierra de Nombre de Dios in tropical lowland rainforest (Tropical Moist Forest formation of Holdridge, 1962).

Population E (3 specimens).—From localities in the Aguan-Negro Plain and the Sierra de Nombre de Dios at elevations from sea level to about 200 m in tropical lowland rainforest and short-tree savanna (Tropical Moist Forest formation of Holdridge, 1962).

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Figure 1. Distribution in Honduras of population samples utilized in this study. See text for description of samples A-K.

Population F (1 specimen).—From one locality in the valley of the Río Tinto at an elevation of about 430 m in tropical lowland rainforest (Tropical Moist Forest formation of Holdridge, 1962).

Population G (3 specimens).—From localities on the Mosquito Coast near sea level in lowland pine savanna (Tropical Moist Forest formation of Holdridge, 1962).

Population H (4 specimens).—From localities near Lake Yojoa at elevations from 700 to 750 m in disturbed or undisturbed broadleaf evergreen forest (Subtropical Wet Forest formation of Holdridge, 1962).

Population I (1 specimen).—From one locality in the Valle de Comayagua at an elevation of 580 m in open thorn forest (Tropical Arid Forest formation of Holdridge, 1962).

Population J (7 specimens).—From localities in or near the Valle de Yeguaré at elevations from 800 to 1000 m in mixed scrub forest (Subtropical Dry Forest formation of Holdridge, 1962).

Population K (1 specimen).—From one locality in the Pacific lowlands at an elevation near sea level in

dense scrub forest (Tropical Dry Forest formation of Holdridge, 1962).

ANALYSIS OF VARIATION

Snakes of the genus *Micrurus* are notorious for the small number of external distinguishing features. Dorsal scale row number and the condition of the head scales and the anal plate are all invariant. Diagnoses of the subspecies of *Micrurus nigrocinctus* have utilized the following characters: numbers of ventrals, position of the nuchal band, numbers of black body bands, presence or absence of yellow bands, and condition of the black tipping on the scales of the red bands. It is the variation in these characters as well as the variation in the number of subcaudals and the size of the black head cap in the Honduran specimens with which we are here concerned.

Scutellation.—Coral snakes are highly sexually dimorphic in ventral and subcaudal numbers, with females having the greater number of ventrals and males the greater number of subcaudals.

In Honduras, there appears to be a tendency for both males and females from the southern portion of the country to have higher numbers of ventrals, although this trend is not well documented (Table 1). Variation in subcaudal number is limited and exhibits no discernible pattern (Table 1).

Black body band number.—The number of black body bands in *Micrurus nigrocinctus* over the entire range of the species varies from 10 to 29. The range of Honduran specimens is almost the same, 11 to 29. Variation in black band number appears to be of no geographic significance. Both the highest and lowest ring numbers occur in the department of Atlántida in northern

TABLE 1. Variation in ventrals and subcaudals in Honduran *Micrurus nigrocinctus*. Population statistics are arranged as follows: range (mean) sample size.

Population	Ventrals		Subcaudals	
	Males	Females	Males	Females
A	190–203(198.4)9	208–220(213.0)13	47–51(49.6)8	34–42(37.6)12
B	191–206(196.8)13	206–217(210.4)9	46–52(49.3)8	34–39(36.4)9
C	193–202(198.6)5	206–217(212.5)8	45–51(47.0)5	32–39(36.8)6
D	198	208	45	36
E	190–201(195.5)2	210	49–51(50.0)2	37
F	203	—	46	—
G	200–202(201.0)2	211	54–56(55.0)2	—
H	208	215–218(216.5)2	50	36–39(37.7)3
I	201	—	46	—
J	191–206(200.0)4	218–224(220.6)3	42–50(47.5)4	34–43(38.0)3
K	207	—	51	—

TABLE 2. Variation in black body band number in Honduran *Micrurus nigrocinctus*. Population statistics are arranged as follows: range (mean) sample size.

Population	Males	Females
A	13-24(17.6)9	14-23(19.1)13
B	11-21(13.8)13	11-20(16.3)11
C	15-19(17.4)5	16-21(18.6)8
D	27	29
E	14-20(17.0)2	22
F	25	—
G	18-19(18.5)2	23
H	20	17-22(19.0)3
I	22	—
J	18-19(18.5)4	18-20(19.0)3
K	15	—

Honduras, whereas, intermediate numbers are found elsewhere (Table 2). A single specimen (MCZ 32011) has a saddle pattern as has been described for *Micrurus fulvius* (Neill, 1963).

Yellow body bands.—Only a few of the specimens examined have retained the original color distinction between the red and yellow bands sufficiently intact so that an accurate determination of the length of the yellow bands can be made. It is apparent, nevertheless, that the yellow bands range in length from 0 to 2 scales. Yellow bands appear to be absent in all representatives of populations D, E, and F (Roze's, 1970, comments to the contrary notwithstanding). Yellow bands are present in all representatives of populations C, G, H, I, J, and K (Figs. 2A and 3A). Most of the specimens comprising population B appear to have had yellow bands, although in about 7 specimens they appear to have been absent. These specimens are all old and faded and no fresh material is available to corroborate these statements. Within population A some specimens are bicolor (5 of 23 specimens) and some are tricolor (at least 13 of 23 specimens still show evidence of yellow bands). The change between these two conditions is not abrupt, as is demonstrated in a series of 11 specimens from the vicinity of La Lima in the private collection of John Dickson. Three specimens are bicolor, showing no evidence of yellow bands. Seven specimens are tricolor and the yellow bands range from 1 to $1\frac{1}{2}$ scales in length. Three other specimens show various stages of intermediacy between the bicolor and tricolor conditions. In these specimens yellow bands are absent or ill-defined on some amount of the posterior portion of the body.

Black tipping on scales of red bands.—In *M. nigrocinctus* throughout its range, black pigment

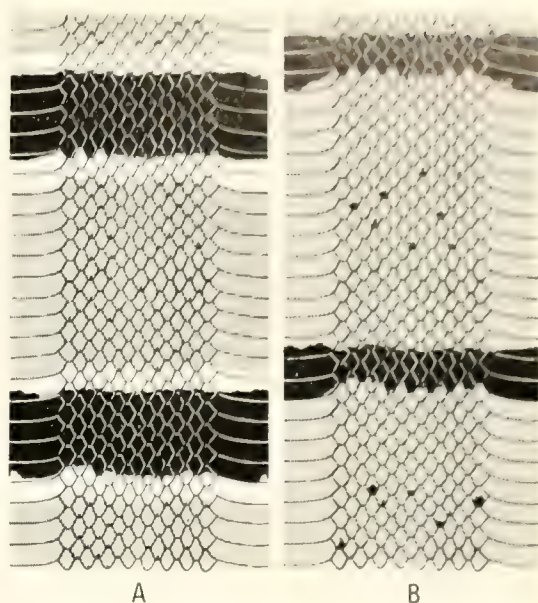


Figure 2. Dorsal color pattern of (A) LSUMZ 24423 from 4 miles N San Lorenzo, Depto. Valle, Honduras and (B) LSUMZ 22451 from the mountains above Trujillo, Depto. Colón, Honduras.

distribution within the red rings varies from pigment being absent to being present and evenly distributed (approximately one spot per scale) to being present and unevenly distributed (some spots occupy more than one scale). Subspecies of *M. nigrocinctus* have been partially diagnosed on the basis of the type of pattern of black pigment deposition (Roze, 1970). *Micrurus n. zunilensis* Schmidt, *M. n. coibensis* Schmidt (Isla de Coiba, Panamá), and *M. n. melanocephalus* (Hallowell) (Pacific versant of Nicaragua and Costa Rica) have very little, if any, black pigment present on the scales of the red bands. *Micrurus n. nigrocinctus* (Girard) (Pacific versant of southern Costa Rica, Panamá, and adjacent Colombia), *M. n. mosquitensis* Schmidt (Atlantic versant of eastern and southern Nicaragua to northwestern Panamá), and *M. n. babaspul* Roze (Isla del Maiz, Nicaragua) have well-defined black spots present on the tips of each of the scales of the red bands. *Micrurus n. divaricatus* has a relatively large amount of black pigment irregularly distributed on the scales of the red bands.

The amount of variation in black pigment distribution in specimens of *M. nigrocinctus* from Honduras is so great as to coincide with the range of variation for the entire species. Variation is up seven pattern categories in the

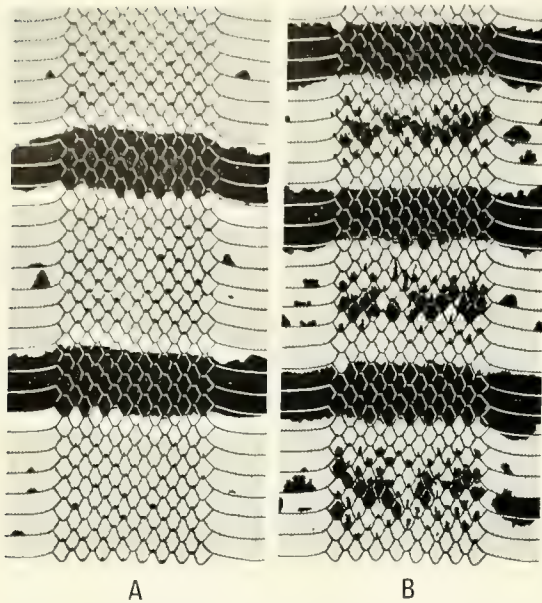


Figure 3. Dorsal color pattern of (A) LSUMZ 24422 from Tancin, Depto. Gracias a Dios, Honduras and (B) FMNH 8083 from the Garcia Plantation, Depto. Yoro, Honduras.

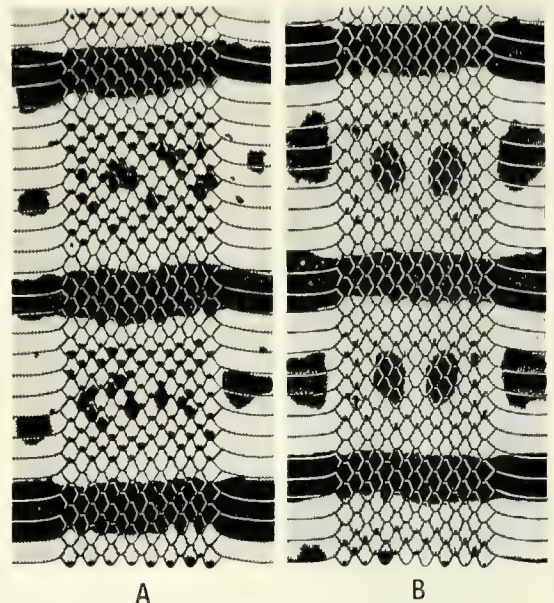


Figure 4. Dorsal color pattern of (A) USNM 20282 and (B) USNM 20283 from Patuca, Depto. Gracias a Dios, Honduras.

the spectrum of variation for facility of discussion. The pattern categories may be characterized as follows.

1. Black pigment on the red bands is absent, indistinct, or restricted to a few scattered scales (Fig. 2A, B).

2. Black tipping is present and more or less uniform on all scales of the red band (Fig. 3A).

3. Black pigment is scattered and some is clumped into larger spots, but tends to be arranged in the middle of the band (Fig. 3B).

4. Black tipping is present on all scales of the red bands but some black tips are fused to form larger spots covering one or two dorsal scales (Fig. 4A).

5. Black pigment is scattered all over the red band, but pigment fusion has produced definite paravertebral accessory incomplete bands; a black spot or scattered black pigment may be present on the venter opposite the dorsal spots (Fig. 4B).

6. Black pigment of red bands is restricted to lateral accessory incomplete bands (Fig. 5A).

7. Accessory incomplete bands fused to form a complete band analogous to the primary black bands (Fig. 5B).

Pattern 1 is characteristic of *M. n. zunilensis* and perhaps *M. n. coibensis* and *M. n. melanocephalus*. Pattern 2 characterizes *M. n. nigrocinctus*, *M. n. mosquitensis*, and *M. n. babaspul*, and patterns 4 and 5 are found on *M. n. divari-*

catus. Patterns 3 and 5 have not been previously described. The single specimen exhibiting pattern 7 is discussed below. Distribution of the 7 pattern types among the 11 populations is shown in Table 3.

Several features are apparent in the distribution of color patterns (Table 3). First, patterns 1, 2, and 4 are relatively widespread geographically. They are also represented in the majority of the specimens. Patterns 3, 5, 6, and 7 are restricted

TABLE 3. Distribution of the types of black pigment deposition on the red bands in Honduran *Micrurus nigrocinctus*.

Population	Pattern types						
	1	2	3	4	5	6	7
A	8	10	—	4	1	—	—
B	7	12	—	3	1	—	—
C	1	9	—	3	—	—	—
D	—	—	—	—	—	1	1
E	1	—	2	—	—	—	—
F	—	—	1	—	—	—	—
G	—	1	—	—	2	—	—
H	3	—	—	1	—	—	—
I	1	—	—	—	—	—	—
J	4	3	—	—	—	—	—
K	1	—	—	—	—	—	—
Total	26	35	3	11	4	1	1

to the more northern portions of the country and are represented in very few of the specimens. The populations with the largest number of members exhibit the widest range of pattern types. Thus, caution is required in drawing conclusions about the significance of these pattern types and their distribution because of the biased samples. Nevertheless, patterns 6 and 7 are known only from population D. Also, patterns 1, 2, and 4 are found to the exclusion of other pattern types in the southern populations (H through K).

Position of the nuchal band and the size of the black head cap.—The position of the anterior edge of the nuchal band in Honduran *M. nigrocinctus* ranges from 2 dorsal scale lengths posterior to the parietals to $1\frac{1}{2}$ dorsal scale lengths onto the posterior edge of the parietals. The black head cap may occupy as little as the internasals and prefrontals or as much as the internasals, prefrontals, frontal, supraoculars and the anterior one-fourth of the parietals. The size of the light head band is a reflection of the size of the black head cap and the position of the nuchal band, and is shortest in populations G, I, J, and K, longest in populations B, C, D, E, and F, and of intermediate size in populations A and H.

STATUS OF THE MAINLAND SPECIMEN OF "*MICRURUS RUATANUS*"

Roze (1967) reported *M. ruatanus*, formerly known only from the Bay Islands of Honduras, from the adjacent mainland of Honduras on the basis of TCWC 21181 from $5\frac{1}{4}$ miles east of La Ceiba, Depto. Atlántida. This record has been questioned by Meyer (1969) and Wilson and Hahn (in press). We have examined this specimen and consider it to represent *nigrocinctus* and offer the following explanation to account for its resemblance to *Micrurus ruatanus*. In size and habitus TCWC 21181 resembles *nigrocinctus*. It measures 734 mm in total length, a size approximated by numerous *nigrocinctus* from Honduras, whereas the largest *ruatanus* from the Bay Islands known to us measures 620 mm. The head of adult *nigrocinctus* from the northern coast of Honduras is most often well distinct from the neck, whereas that of *ruatanus* is scarcely distinct from the neck; the La Ceiba specimen resembles *nigrocinctus* in this respect.

The number of black body bands (29) on TCWC 21181 is lower than that recorded for any *ruatanus* from the Bay Islands (the range is 34 to

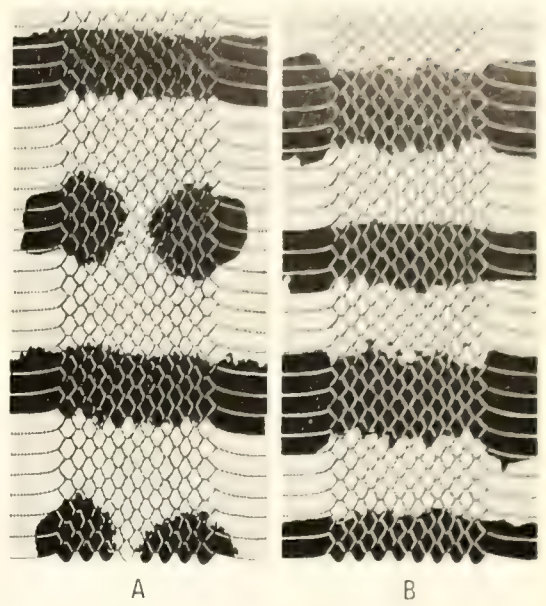


Figure 5. Dorsal color pattern of (A) LSUMZ 21773 from the mountains above Corozal, Depto. Atlántida Honduras and (B) TCWC 21181 from $5\frac{1}{4}$ miles E La Ceiba, Depto. Atlántida, Honduras.

45 according to Schmidt, 1933, and a range of 33 to 45 is given for 8 specimens examined by Wilson and Hahn, in press).

The ventral count for TCWC 21181 (a female) is 208, within the range of 207 to 220 given for *M. n. divaricatus* by Schmidt (1933, 1936), but not within that recorded for females of *ruatanus* (Günther, 1895, recorded a range of 200 to 204 and Wilson and Hahn, in press, a range of 193 to 203).

The resemblance of TCWC 21181 to *M. ruatanus* in pattern, particularly in the relatively high number of black body bands, is only superficial. The specimen appears to have been bicolor in life, as is the case with fresh material from this general area of Honduras and with *M. ruatanus*. Nevertheless, the black body bands of *ruatanus* are alternately longer and shorter and the shorter ones are frequently interrupted laterally, especially on the posterior portion of the body (Schmidt, 1933; Wilson and Hahn, in press). On the other hand, the bands of TCWC 21181 are all about the same length (Fig. 5B) and none are broken. We suggest that this specimen, with its high number of black body bands (for *nigrocinctus*), represents the end stage of a morphological series of increasing development and concentration of pigment. We envision this morphological series

nate in a condition that we have designated as pattern 2, where black tipping is uniformly distributed on all scales of the red band. This cline continues through pattern 4, where some black tips are fused together to form larger spots, and patterns 5 and 6, where either paravertebral or lateral accessory incomplete bands are present. The cline ends with pattern 7 (that of TCWC 21181), where the accessory bands are complete. Complete fusion of accessory bands would almost double the number of bands. If the number of accessory bands of TCWC 21181 is subtracted from the total number of 29, the number of primary black bands is 15, a number within the range of *nigrocinctus*, as envisioned by Schmidt (1933). It is worthy of note that patterns 4, 5, and 6 are most frequently or solely encountered in the populations on the northern coast of Honduras. We suspect that additional collecting in the area around and between La Ceiba and Trujillo will demonstrate the presence of specimens with patterns intermediate between those designated as patterns 5 and 6.

In conclusion, we feel that TCWC 21181 from near La Ceiba, Honduras is a *M. nigrocinctus*, albeit a peculiar one, and that *M. ruatanus* is not known from the mainland of Honduras.

GEOGRAPHIC TRENDS AND SYSTEMATIC CONCLUSIONS

Although the characters examined in this study exhibit patterns that are discordant, the populations of the north coast of Honduras (B, D, and E) are distinct from the populations of southern Honduras (I, J, and K) in a number of features. The populations from intermediate areas exhibit discordant intermixtures of these characters. Specimens from northern Honduras generally are bicolor and have a low number of black body bands and ventrals and a long pale head band. Specimens from southern Honduras generally are tricolor with a high number of black body bands and ventrals and a short pale head band.

In Honduras, at least, we see no reason to recognize infraspecific taxa. Such an action would require an entirely arbitrary decision as to which of the characters we have studied is most important (*i.e.*, most representative of the genetic relationships) and we have no confidence in making such a judgment. In addition, the "zone of intergradation" is larger than the range of either the northern or southern populations. Finally, we would like to have the opportunity to examine

sufficient material from other sites before extending our remarks further than we have here.

MATERIAL EXAMINED

For easy reference, we have arranged the specimens examined under the 11 populations we recognize.

Population A.—ATLÁNTIDA: Berichiche (MCZ 38773); Guaymas District (FMNH 16116–20); Ulua River, near Tela (MCZ 19945). CORTÉS: Lake Ticamaya (FMNH 5311); La Lima (LSUMZ 24425; JD-11); W of San Pedro Sula (FMNH 5312); 15.5 mi S Puerto Cortés (LSUMZ 24426). YORO: García Plantation (FMNH 8083).

Population B.—ATLÁNTIDA: Lancetilla (AMNH 46968–71, 70237–38; FMNH 21783; MCZ 29412–13, 32010–12, 32014, 33342, 38772–73); Colorado District (FMNH 16115; MCZ 21772–73); Tela (FMNH 16115, 25215; USNM 82166, 84568–69, 129428).

Population C.—YORO: Mataderos Mountains (MCZ 38770–71); Portillo Grande (FMNH 21893–94, 34720–22, 34747, 35559; MCZ 38774–77).

Population D.—ATLÁNTIDA: mountains above Corozal (LSUMZ 21773); 5¼ mi E La Ceiba (TCWC 21181).

Population E.—COLÓN: Puerto Castilla (MCZ 22433–34); mountains above Trujillo (LSUMZ 22451).

Population F.—OLANCHO: 2 km SW Dulce Nombre de Culmí (LACM 45179).

Population G.—GRACIAS A DIOS: Patuca (USNM 20282–83); Tancin (LSUMZ 24422).

Population H.—CORTÉS: Agua Azul (AMNH 70157, 70216–17); 2 mi N El Jiral (LSUMZ 24424).

Population I.—COMAYAGUA: Comayagua (AMNH 70155).

Population J.—FRANCISCO MORAZÁN: Las Mesas (AMNH 70156); slopes of Cerro Uyuca (AMNH 70204); El Zamorano (AMNH 70153; MCZ 49889–92).

Population K.—VALLE: 4 mi N San Lorenzo (LSUMZ 24423).

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We also extend our gratitude to John Dickson of La Lima, Honduras for the opportunity to examine specimens in his personal collection and to Diana Dee Dugas for her help in gathering data.

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A NEW SPECIES OF ROCK DWELLING DENDROCHIROTE HOLOTHURIAN FROM CATALINA ISLAND

JOSEPHINE YUDKIN YINGST¹

ABSTRACT: A new species of the genus *Cucumaria* Blainville (1830) is described from Santa Catalina Island. It is a filter feeder and occurs abundantly nestled in subtidal rock reefs. It is distinct from other members of the genus described from the Pacific coast of North America in its coloration, spicule types, and internal anatomy.

An undescribed species of *Cucumaria* Blainville (1830) was found to be abundant in subtidal rock reefs at Santa Catalina Island (lat. 33° N—long. 119° W) which lies off the coast of southern California. The species is unique in its habit of nestling deep into rock crevices. These cucumbers differ greatly in size, color, internal anatomy and spicule types from other species of *Cucumaria* known from the Pacific coast of North America, namely *C. crax* Deichmann, 1940, *C. curata* Cowles, 1906, and *C. vegae* Theel, 1886. A description of the genus *Cucumaria* may be found in Deichmann (1941).

CLASS: HOLOTHUROIDEA

ORDER: DENDROCHIROTA

GENUS *CUCUMARIA* BLAINVILLE (1830)

Cucumaria salma, new species

Material: Holotype (AHF Echinoderm Collection No. 61), total length 6 cm (contracted) and 3 paratypes (AHF Echinoderm Collection) were collected at a depth of 14 m on the north face of Bird F.

¹ Allan Hancock Foundation, University of Southern California, Los Angeles, California.

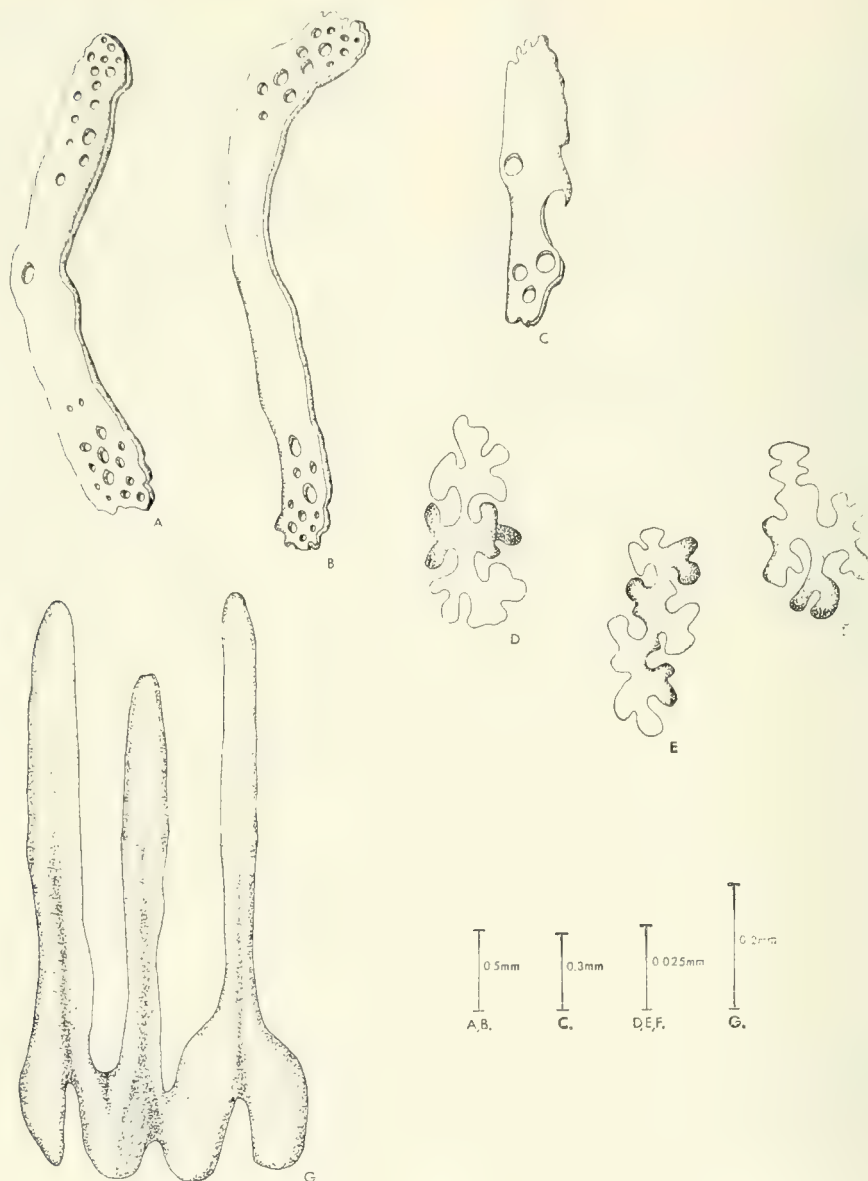


Figure 1. A, B, supporting rods from tentacles; C, perforated plates from tentacles; D, E, F, rosettes from tentacles; G, calcareous ring.

Santa Catalina Island. The animals were concealed in rock crevices and removed by use of a geologist's pick.

Description: Ten dendritic tentacles of equal size form a single circlet bordering the buccal membrane. Retractable tube feet arranged in pairs along and restricted to the ambulacra. Ventral and dorsal ambulacra not differing markedly from each other.

Calcareous ring with distinct posterior projections and long anteriorly projecting processes (Fig. 1G); interradials and radials fused; anterior processes of

the radials distinctly cleft. Four Polian vesicles present. Three or four short stone canals, 3–4 mm in length grouped near the dorsal mesentery or more distantly spaced from each other on the ring. Each canal terminates in a slightly elongate madreporite.

Gonad composed of numerous elongated unbranched tubules united in one basal tuft attached to the dorsal mesentery. Gonoduct opens to exterior directly behind tentacles in central dorsal interambulacrum.

Spicules smooth, without knobs. Body wall spicules with two types of perforated buttons (Fig. 2F–H), and

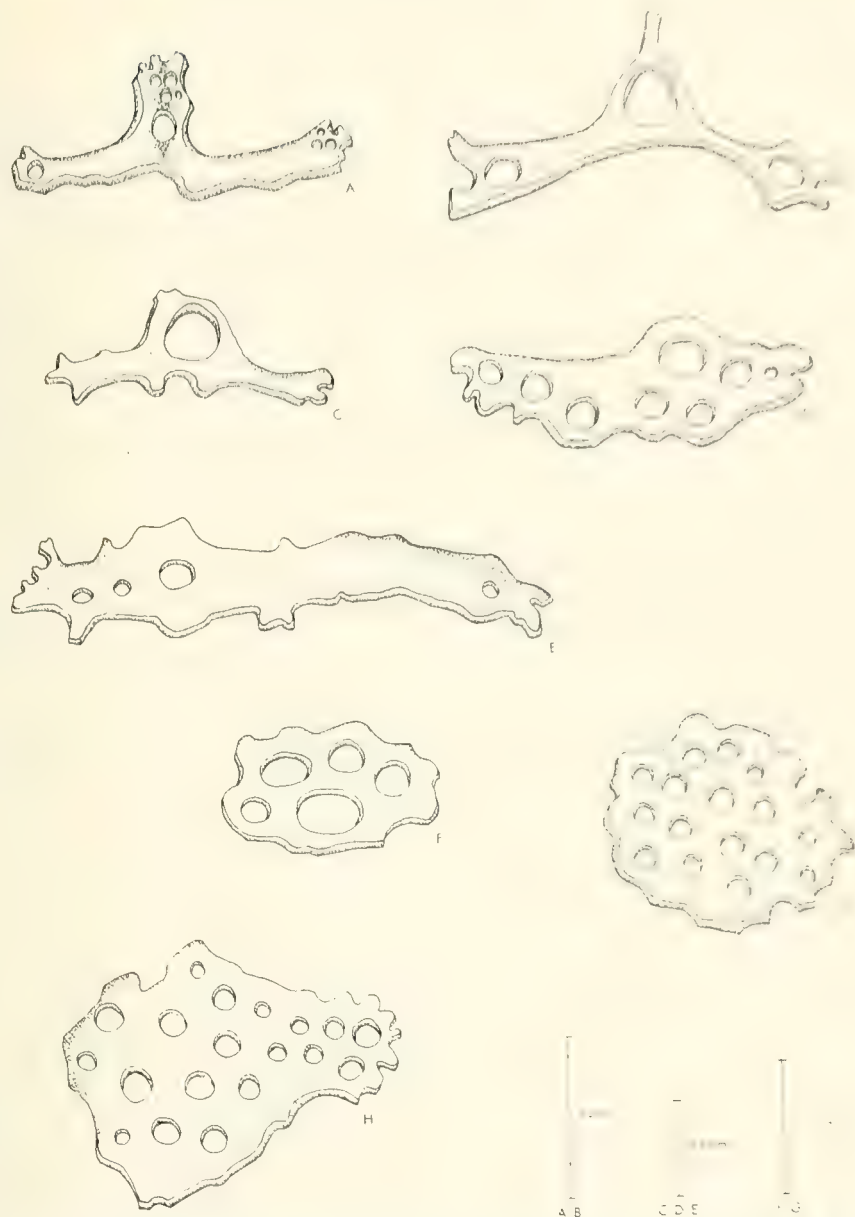


Figure 2. A, perforated three-armed rod from introvert; B, C, supporting rods from tube feet; D, E, perforated plates from tube feet; F, G, H, perforated buttons from body wall.

perforated rods (Fig. 3F), three-armed perforated rods (Fig. 3A, E), and perforated plates (Fig. 3B-D). Tube feet with a small number of slender supporting plates (Fig. 2D, E) and three-armed rods (Fig. 2B, C); when perforated usually a small number of openings. No indication of end plates. Spicules of introvert distinct from those of tentacles, resembling those of body wall, consisting of three-armed perforated rods and perforated plates (Fig. 2A). Tentacles with numerous large narrow rods with perforated ends

(Fig. 1A, B), smaller perforated plates (Fig. 1C), and very small rosette-like plates with irregular marginal processes (Fig. 1D-F).

Color: Primarily salmon with a concentration of black pigment toward the anterior end. Introvert, buccal membrane, and tentacles mottled with white and black patches of pigment; tentacular papillae black.

Measurements: Length of relaxed specimens about 10 cm.

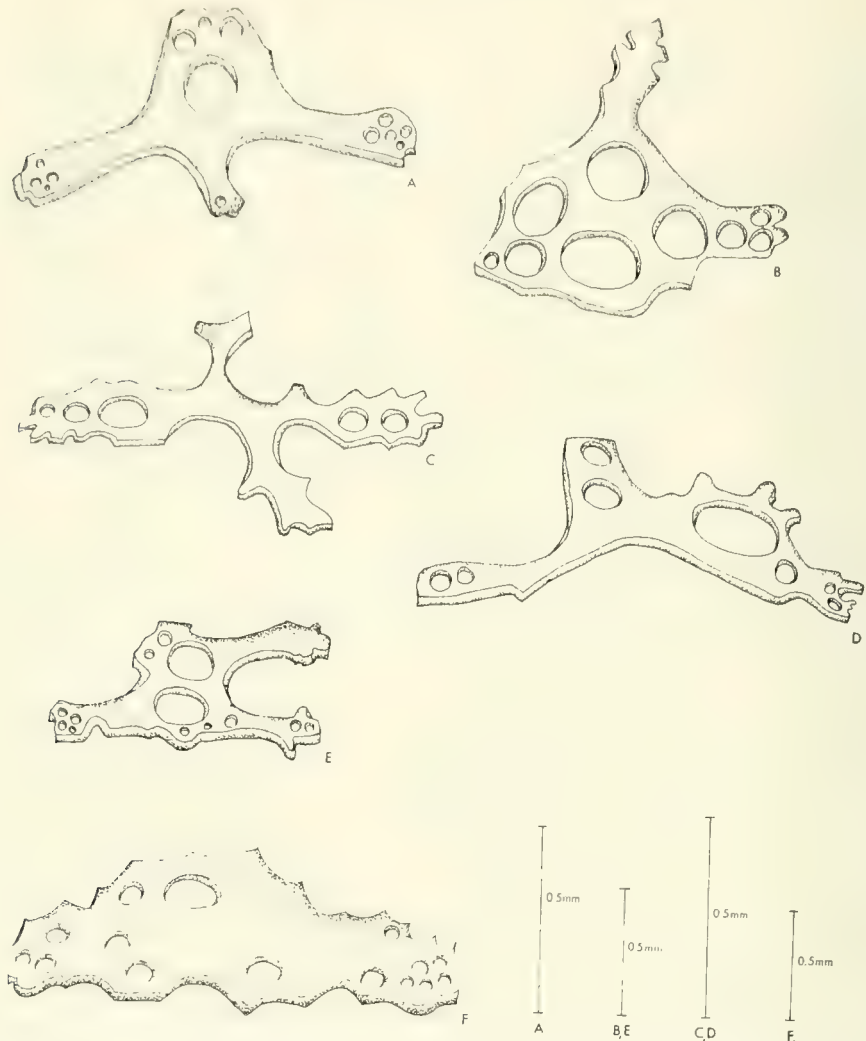


Figure 3. A, E, perforated three-armed rods from body wall; B, C, D, perforated plates from body wall; F, perforated rod from body wall.

Distribution: Known from Santa Cruz Island, Santa Barbara County (Given, pers. comm.) to Point Loma, San Diego County (Turner, Ebert, and Given, 1968). Occurs at depths of 3 to 20 m in rocky reefs.

Observations: The aborescently branching tentacles are highly retractile. The papillae on the tentacles project above the epithelium and are independently retractile. These papillae are adhesive and used to collect food particles.

The tube feet nearest the base of the tentacles can elongate to a length of 3 mm. Retracted holothurians utilize their tube feet to pick up particles from the substrate and to transfer them into the introverted oral end. When the tentacles are extended these anteriormost tube feet may also select

particles from the substrate and transfer them onto the tentacular papillae.

In the field the animals nestle in the rock crevices and extend their tentacles to catch suspended particulate matter. The body wall is extremely plastic, which permits the cucumbers to wedge themselves into crevices deeper in the rock and away from the rock face.

Remarks: *Cucumaria salma* [*salma* from Latin *salmo* = salmon] is suggested because of the principal color of the cucumbers.

Panning (1949, 1951, 1962) revised the genus *Cucumaria* and incorporated into other genera several of the species referred to by Deichmann (1941) from the Panamic region and by Clark

TABLE 1. Comparison of west coast species in the genus *Cucumaria*

<i>C. curata</i>	<i>C. crax</i>	<i>C. vegae</i>	<i>C. salma</i>
SIZE			
Up to 2.5 cm; ventrum flat	Small, 1.5 cm (contracted)	Small, 3.8 cm; ends tapered	Medium, 10 cm
TENTACLES			
Unequal	Equal, bushy	Unequal	Equal, bushy
TUBE FEET			
Few; double row in dorsal ambulacrum	Large; retractile; only in ambulacra	Double row; in interambulacra	Retractile; double row; only in ambulacra
CALCAREOUS RING			
Well-developed	Simple; post. prolongations	Slender; no post. prolongations	Post. prolongations; ant. processes w/cleft
STONE CANAL/POLIAN VESICLES/GENITAL PAPILLAE			
1/1/none	1/2/?	1/1/5	3-4/4/none
SPICULES-BODY			
Perf. buttons, 4, 6 holes, undulated margins; plates few, 20+ holes	Buttons, 4-8 marginal holes, not all entirely closed	Few, smooth rods, 1-3 holes in each end	Smooth perf. rods and buttons; plates
SPICULES-TUBE FEET			
No end plate; few supp. rods	Rudimentary end plate; three-armed supp. rods	Fragment of end plate, or none; no supp. rods; smooth plates w/undulating margins, varying no. of holes	No end plate; few supp. plates; three- armed rods w/few holes
SPICULES-TENTACLES AND INTROVERT			
Numerous supp. rods	Tent.; buttons intro.; numerous rods w/ perf. ends	—	Tent.; large rods w perf. ends; perf. plates; minute rosettes intro.; three- armed rods
COLOR			
Dorsum and tent. purple brown; vent. and oral disc yellow	Mottled brown body; ambulacra lighter; tent. black	Vent. yellow, gray; body ends brown	Body salmon; intro. and tent. mottled; tent. podia black
DISTRIBUTION			
Intertidal, rocks, mussel beds, central California	Sand, west coast Baja California-South America	Intertidal rock crevices, north Pacific coast	Rock crevices. 3-15 m deep, southern California

(1901a, 1901b) from the Pacific coast of North America as *Cucumaria*. Panning (1949) changed the species *C. dubiosa* Semper, 1868, to *Pseudocnus dubiosus* and in 1964 he changed *C. californica* Semper, 1868, to *Pseudocnus californicus*. Stimpson (1964) changed *Cucumaria populifera* to *Pentamera populifera* Panning (1949). Pawson (pers. comm.) suggests that *Cucumaria miniata* Brandt, 1835, *C. lubrica* Clark, 1901, and *C.*

piperrata Stimpson, 1864, do not belong in the genus *Cucumaria* and probably should be placed in the genus *Pseudocnus*.

Cucumaria salma is easily distinguished from the remaining three species *C. crax*, *C. curata*, and *C. vegae*; all of which are found on the Pacific coast of North America. *Cucumaria salma* is about 10 cm in length; has three or four stone canals; four Polian vesicles; is salmon colored; and

has distinct spicules. The latter three species range in size from 1.5–4 cm; have one stone canal; one or two Polian vesicles; and are gray or brown in color (Table 1).

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A NEW SPECIES OF SEA OTTER FROM THE LATE PLEISTOCENE OF NORTHWESTERN CALIFORNIA

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ABSTRACT: A new species of sea otter is described from a Late Pleistocene marine deposit, Humboldt County, California. The species is closely related to the living sea otter, *Enhydra lutris*, but differs significantly in possessing larger P_3 , P_4 , M_1 , and presumably M_2 , shorter ascending ramus with respect to total length of mandible, and a more simply formed angle. Proportions of the mandible suggest that the skull of the new species may have been slightly longer and lower than that of *E. lutris*. No special affinities with particular living populations of *E. lutris* are recognized.

The prior fossil records of sea otter in the north-eastern Pacific has, with but one exception, included only postcranial elements and all fossil discoveries have occurred in two widely separated areas, Oregon and southern California. The Oregon record consists only of a right femur of Pleistocene age from the Elk River Formation

(Leffler, 1964). The southern California records (Mitchell, 1966) include a lower, deciduous tooth of Early Pleistocene age from the Timm's Point Silt, a right humerus of Late Pleistocene age from

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the Palos Verdes Sand, and various limbs and vertebral elements from Late Pleistocene deposits of Santa Rosa Island. Leffler referred the Oregon femur to *Enhydra* sp. while Mitchell concluded that all the southern California specimens probably were referable to *Enhydra lutris* (Linnaeus).

In May 1967, a well preserved mandible of a fossil sea otter, lacking only a few teeth, was recovered from a Late Pleistocene marine deposit, located on the Humboldt County coast, northwestern California. The mandible is evidently the first known of a fossil sea otter from the north-eastern Pacific and it provides the first major indication of the cranial morphology of fossil sea otters. The Humboldt County mandible is interpreted to be that of a new species of sea otter referable to the genus *Enhydra*.

The left and right rami of the mandible were discovered at the same locality by different persons at different times. The close morphologic agreement of the two rami and near perfect fit of the symphysis make it virtually certain that they are from the same individual.

GENUS *ENHYDRA* FLEMING, 1822

Enhydra macrodonta, new species

Figures 1 and 2

Holotype: California State University, Humboldt, Department of Geology and Earth Science, specimen No. 745-1, a mandible lacking left P_2 , M_1 , and M_2 ; right incisors and M_2 . The medial projection of both condyles has been broken off.

Type locality: California State University, Humboldt, Department of Geology and Earth Science, locality No. 745. A moderately steep, north-facing, excavated slope located approximately 11 miles north of Arcata, Humboldt County, California, at the junction of U.S. 101 and Crannell Road. The exposure consists of three, nearly flat-lying, sedimentary units including (from bottom to top): 1) a basal 12 feet of gray, medium-grained, pebbly, fossiliferous, semi-consolidated sand; 2) 50 feet of gray, clayey, fine-grained, fossiliferous sand; and 3) 70 feet of light-brown, medium-grained, semi-consolidated, pebbly sand.

The rami were found, as float, lying on the exposed surface of the gray clayey sand unit. The left ramus was found in a narrow gully at the foot of the excavated slope about 230 feet east of the centerline of Little River Road (the frontage road for U.S. 101). The right ramus was found directly upslope from the left ramus a distance of approximately 25 feet. The gray, clayey sand matrix adhering to both rami is identical with the lithology of the gray clayey sand unit and it is virtually certain that the two were eroded from this stratigraphic unit.

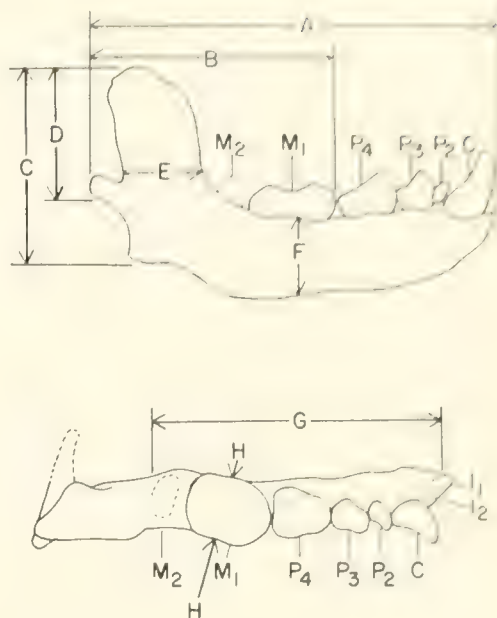


Figure 1. Key to mandibular measurements utilized in this study and presented in Table 1. Dimensions A, B, and D are measured from the posterior margin of the condylar process along the axis of the ascending ramus. All measurements are in millimeters.

Formation: The otter-bearing unit has not been formally described or named and it can be definitely traced only about $\frac{3}{4}$ mile south of the Crannell Road locality. Its relationship with the well known Cenozoic sedimentary sequence (Ogle, 1953) exposed in the Eel River Valley 40 miles to the south is not known. However, reconnaissance mapping and indirect paleontologic evidence suggest that the otter-bearing unit may be older than the Hookton Formation (Late Pleistocene) and either younger or partially equivalent to the Carlotta Formation (Plio-Pleistocene); these formations are in depositional contact with each other in the Eel River Valley sequence.

Age: Late Pleistocene (see discussion below).

Diagnosis: Relative to *Enhydra lutris*, the only other species included in the genus: horizontal rami thick, occlusal outline of P_3 , P_4 , and M_1 approximately $\frac{1}{3}$ larger and plump; M_2 presumably slightly larger based on slightly greater length and width of the alveoli; and ascending ramus short with respect to length of the mandible; angle sharply rounded, right-angled, with ascending and horizontal margins narrow and rounded.

Description and comparison: The close correspondence between the fossil mandible and that of the compared specimens of *Enhydra* (Table 1) with respect to size, shape, and morphology indicates that *E. macrodonta* is closely related to *E. lutris* and is certainly

TABLE 1. Selected mandibular measurements of *Enhydra macrodonta*, new species and *E. lutris*. Key to measurements A-H is given in Figure 1. All measurements are in millimeters.

Spec. No.	Loc.	Species	Growth stage	Sex	M ₂ (alveolus)								M ₁		P ₄		P ₃			
					A	B	C	D	E	F	G	H	L	W	L	W	L	W	L	W
(a) 745-1	Calif.	<i>E. macrodonta</i>	Yng. adult	?	83.9	50.2	41.9	28.0	19.6	18.3	61.4	15.2	6.8	8.7	18.5	15.8	13.4	11.9	8.3	8.9
(b) M71-080	"	<i>E. lutris</i>	Adult	?	90.8	54.8	47.2	33.8	22.6	17.7	60.4	11.2	5.0	7.1	15.5	12.8	11.1	9.2	6.7	6.8
(c) 6902	Alaska	"	Adult	M	90.9	56.3	47.5	37.4	24.0	19.1	56.5	10.7	4.8	5.9	17.7	13.9	12.2	10.5	6.5	7.0
(c) 6801	Calif.	"	Adult	M	81.6	53.4	51.5	38.0	23.7	17.9	54.1	10.6	5.3	8.2	15.6	12.0	10.5	8.9	7.0	4.9
(b) M71-081	"	"	Yng. adult	?	86.1	54.3	45.5	34.2	23.9	18.7	54.1	10.9	4.8	6.8	15.4	13.7	10.7	9.6	6.1	6.9
(b) M71-082	Alaska	"	Adult	F	83.9	50.8	42.2	32.1	21.5	15.7	53.8	10.0	5.3	5.9	15.3	13.9	9.8	9.4	6.4	6.5
(b) M71-083	"	"	Adult	?	83.7	55.1	43.6	32.7	22.8	15.9	53.9	9.5	4.9	5.3	15.2	11.5	10.7	9.0	6.9	5.0
(b) M71-084	"	"	Adult	?	86.4	51.1	43.8	33.1	22.6	16.9	54.8	6.1	5.6	5.6	15.4	12.4	11.6	9.3	Badly worn	Badly worn
(d) 135831	Calif.	"	Adult	M	79.7	35.7	46.2	29.3	19.7	17.8	52.5	11.2	5.3	7.4	15.3	12.7	9.7	8.9	5.7	5.7
(b) M71-085	Alaska	"	Adult	F	86.4	50.4	44.5	33.8	22.6	17.2	54.3	10.6	5.3	6.7	14.4	12.8	10.8	9.4	6.4	5.3
(b) M71-086	"	"	Yng. adult	?	80.1	47.4	39.6	29.7	21.0	15.7	55.1	11.4	5.9	7.3	16.2	12.8	10.8	9.1	7.4	5.4
(b) M71-087	"	"	Adult	?	80.2	48.0	40.6	29.1	21.2	17.4	53.8	12.8	5.3	7.9	16.0	12.9	11.6	9.3	7.1	5.1
(d) 137003	"	"	Juv.	M	77.3	30.6	35.7	22.6	19.4	16.0	53.9	12.6	4.7	7.3	14.9	13.4	10.9	9.5	6.4	6.3
(b) M71-088	"	"	Juv.	?	75.8	45.7	39.5	29.5	18.4	16.9	52.6	12.4	5.3	7.3	17.1	13.4	*11.6	*9.4	7.4	5.9
(b) M71-089	"	"	Juv.	M	79.0	43.6	38.4	28.1	18.6	15.3	54.0	12.3	4.6	8.2	15.4	12.6	*10.8	*9.4	7.4	4.9
(b) M71-090	"	"	Yng. adult	?	75.4	43.4	38.4	28.5	18.3	16.0	53.6	12.7	5.5	7.9	16.7	13.1	11.4	9.6	7.6	5.5
(b) M71-091	"	"	Juv.	F	74.5	41.8	34.4	24.3	18.1	14.0	52.5	13.9	4.3	6.3	15.9	12.4	**	**	7.2	5.5

(a) Calif. State Univ., Humboldt; Dept. of Geology and Earth Science.

(b) Calif. State Univ., Humboldt; Dept. of Zoology.

(c) U. S. Geological Survey, Pacific Coast Center, Menlo Park, Calif.

(d) Univ. of Calif. Museum Vert. Zool., Berkeley, Calif.

L Length.

W Width.

* Milk dentition.

** Unrupted milk dentition.

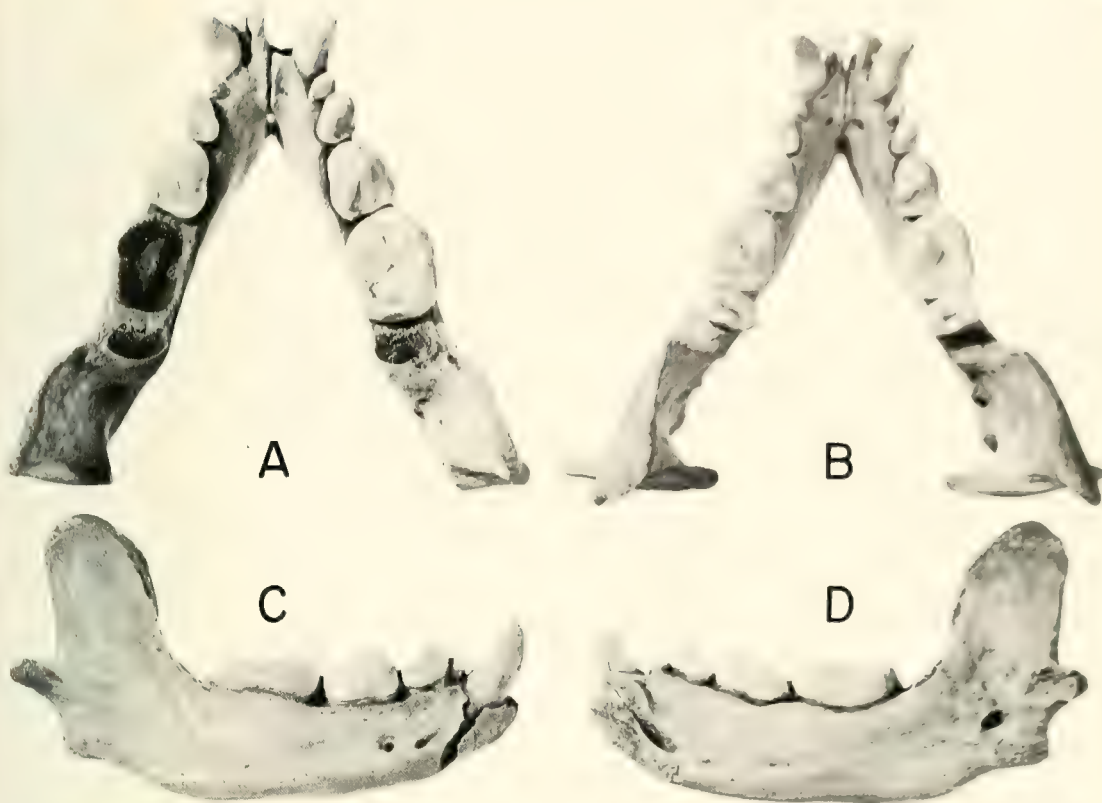


Figure 2. A, *Enhydra macrodonta*, new species; joined left and right mandibular rami, occlusal view (CSUH, Dept. of Geology and Earth Science, No. 745-1). B, *Enhydra lutris* (Linnaeus); mandible, occlusal view (U.S. Geological Survey, No. 6801, adult male, Asilomar State Beach, Monterey Co., California, captured 14 April 1966). C, *Enhydra macrodonta*, new species; right mandibular ramus, lateral view (CSUH, Dept. of Geology and Earth Science, No. 745-1). D, right mandibular ramus, medial view (CSUH, Dept. of Geology and Earth Science, No. 745-1). Scale $1\times$.

the genus *Enhydra*. The presence of permanent dentition coupled with the lack of extensive wear suggests death at an early adult stage of life.

Although the gross morphology of the *E. macrodonta* closely resembles that of *E. lutris* it differs significantly from specimens of comparable or even greater jaw length in that the horizontal ramus is more robust and strongly built, to accommodate the larger teeth, and the tooththrow is proportionately longer. The medial surface of the jaws tends to be rather flat and featureless as in *E. lutris* but the lateral surface differs in being less concave below P_3 – P_4 and substantially more convex below M_1 and M_2 . There are two large, oval-shaped mental foramina on each ramus below P_3 and P_4 on the lateral surface. These foramina are larger than the mental foramina seen in *E. lutris* but their location is essentially the same.

The ascending ramus is more lightly built, more

slender, and shorter than those of *E. lutris* of comparable jaw length. The lateral and medial surfaces of the ascending ramus are essentially parallel and without the surficial irregularities typical of *E. lutris*. The anterodorsal margin of the coronoid crest is narrow and slightly curled medially whereas, in *E. lutris* the margin is more strongly curled and thicker. When the tooththrow is placed in a horizontal position, the anterior edge of the ascending ramus rises at a steep angle and the posterior margin is nearly vertical. In this position the coronoid crest does not project posterior to the condylar process although it overhangs it slightly.

The masseteric fossa is a deeply excavated depression which shallows anteriorly, diminishing to an arrowhead-shaped point. The point is directed anteriorly, not downward as is common in *E. lutris* and terminates just below the posterior

half of M_1 . In *E. lutris* the anterior extremity of the masseteric fossa almost invariably lies below M_2 and occasionally lies below the posterior margin of M_1 . The condyles are about the same size and diameter as the largest specimens of *E. lutris* examined and they are connected to the posterior margin of the ascending ramus by strongly built gussets of bone. The angle consists of a narrow, sharply rounded corner, the posterior and ventral sides of which form an angle of about 90° . The backward-pointing, plate-like structure, which commonly forms the base of the angle in *E. lutris*, is absent in the Humboldt form.

The horizontal angle formed by the medial surfaces of the mandible, when the jaws are placed in the position of "best fit" at the symphysis, measures approximately 63° . Although the magnitude of this angle must be considered only an estimate, since the jaws were not found articulated, it is close to a number of adult specimens of *E. lutris* in which the same angle ranged from 56° to 60° (Fig. 2A, B).

Although the tooththrow in *E. macrodonta* is significantly longer than in those specimens of *E. lutris* having comparable jaw length (Table 1), the teeth in the fossil are spaced and individually oriented in the jaws almost identically to those of the living species. The line of teeth form a fairly well-pronounced arc which bows outward in occlusal view. Whether this curvature is a reflection of growth stage or is a constant character is not certain; in adult *E. lutris* curvature of the tooththrow also occurs but it seems to be much less pronounced (Fig. 2A, B).

The M_2 is lost in both left and right jaws of *E. macrodonta* but the alveoli are well-preserved and their size (Table 1) suggests that M_2 was slightly larger than that found in *E. lutris*. The alveolus of M_2 lies in a large, rounded bulge which swells medially from the base of the anterior edge of the ascending ramus. The alveolus is positioned considerably higher than that for the M_1 . Its shape and orientation suggest that it was occupied by a single-rooted, ovate tooth, whose long axis was oriented transversely to the jaw and whose occlusal surface tilted forward at a moderate angle. The general orientation and position of the alveolus in *E. macrodonta* closely resembles that found in specimens of *E. lutris* in which the growth stage is considered to be late juvenile/early adult.

The M_1 is a bunodont tooth with the cusps arranged in a pattern almost identical to that of *E. lutris*. The tooth width and the distance between the protoconid and metaconid are, however, proportionately greater, and the occlusal area is

about $\frac{1}{3}$ larger. The alveolus for M_1 in the left jaw is figure-eight shaped in occlusal outline. Near its center there are distinct inward projections of bone, one of which connects to a centrally located transverse ridge. This suggests that the alveolus was divided into anterior and posterior sockets as is standard in *E. lutris*.

The P_4 of *E. macrodonta* is approximately $\frac{1}{3}$ larger in occlusal area than that of *E. lutris*. The constriction of the root, evident below the enamel base and above the alveolar margin, suggests that the tooth possesses two roots as in *E. lutris*. The occlusal morphology of the P_4 closely resembles that of *E. lutris* except that in *E. lutris* the ridge radiating posteriorly along the lateral side of the tooth is larger and developed into a more distinct cusp-like structure.

The P_3 in *E. macrodonta* has nearly twice the occlusal area of that in *E. lutris*. It is about $\frac{1}{3}$ the size of P_4 but is similar in occlusal outline, the major exception being a more sharply rounded anterior corner. The low ridge on the medial side of the tooth is proportionately larger in *E. lutris* and it tends to be more inflated and cusp-like. The tooth is oriented as in *E. lutris* but does not appear to lean outward and overhang the jaw as is frequently the case in *E. lutris*.

The P_2 is about $\frac{1}{6}$ the size of P_3 and is only slightly larger than P_1 in *E. lutris*. The long axis of the tooth crosses the jaw axis at an angle somewhat greater than in P_3 . The tooth does not appear to be directed laterally nor to overhang the jaw to the degree as in *E. lutris*. A single, nearly round alveolus in the left jaw indicates that the tooth possessed one root, as in *E. lutris*.

The canine is almost identical in size and form to the canine in *E. lutris*. The first lower incisor of *E. macrodonta* is a long, slender tooth of which nearly half is exposed root. The cutting edge of the enameled surface is bluntly wedge-shaped, with the long axis oriented transverse to the jaw axis. The second lower incisor tightly fills a narrow space between I_1 and the canine. The wedge-shaped crown is about twice the length as that of I_1 . Taken as a group, the close alignment of the canines and incisors suggest that the bite of the animal was effective across the entire anterior margin of the mandible. The incisors show very close correspondence in size to those in *E. lutris*.

DISCUSSION AND CONCLUSIONS

Taxonomic assignment: *Enhydra macrodonta* is assigned to the genus *Enhydra* because of its close

resemblance to *E. lutris* in both mandibular and dental morphology. It consistently and significantly differs from known or examined mandibles of *E. lutris* in the following features: 1) greater size of P_3 , P_4 , M_1 , and possibly M_2 ; 2) longer toothrow; 3) a sharply-rounded angle formed of ascending and ventral margins which are narrow and rounded; and 4) shorter ascending ramus with respect to total length of mandible. These differences are interpreted as justifying the assignment of this fossil mandible to a new species.

Other morphologic characters which are, to some extent, duplicated in specimens of *E. lutris* include: 1) the masseteric fossa extends anteriorly to a point beneath the posterior half of M_1 , and is anteriorly directed; 2) M_2 occupies a large, medially directed swelling, partially hidden from lateral view by the ascending ramus; 3) the medial and lateral surfaces of the ascending ramus are essentially smooth and without bulges or depressions; and 4) the margin of the coronoid crest is narrow and curled only slightly medially. These four characters may represent a transitional stage in growth or perhaps relate to sex and are, therefore, considered to be of questionable diagnostic value at this time.

Morphologically *E. macrodonta* is sufficiently close to *E. lutris* to indicate that the two species are closely related. However, the larger teeth and thicker jaw of *E. macrodonta* seem to suggest that *E. lutris* was, perhaps, not derived directly from *E. macrodonta*, but rather that the two species represent separate lineages which presumably had a common origin prior to the Late Pleistocene. One cannot rule out the possibility, however, that selection toward a "small-toothed" *E. lutris* might have occurred from a "large-toothed" *E. macrodonta*. If this selection did occur then the general tendencies during the evolution of *E. macrodonta* to *E. lutris* would have included: 1) reduction in size of P_3 , P_4 , M_1 , and possibly M_2 , with proportionately greater reduction in tooth width; 2) reduction in the thickness of the jaw below P_3 , P_4 , and M_1 ; 3) reduction in the length of the toothrow; 4) increase in the overall size and complexity of the ascending ramus; 5) increase in height of the ascending ramus with respect to total mandibular length; 6) development of stronger muscle attachments at the angle and ventral margin of the ramus; 7) maintenance of the same general size of incisors, canines, and P_2 ; and 8) maintenance of about the same orientation of the long axes of premolars and molars in occlusal view.

The suggestion by Fisher (1941), that the mandible in *E. lutris* might reflect an evolutionary

process tending to progressively shorten the mandible, is generally supported by the present study. If, as Fisher suggested, the teeth have been progressively crowded together during the evolution of sea otters, so that their long axes now assume variable angles as they do in *E. macrodonta*, then that process probably began before the Late Pleistocene.

Enhydra macrodonta does not appear to retain characters which might provide clues into the pre-Pleistocene evolution of sea otters, nor does it seem to offer a test of the hypothesis suggested by McLaren (1960) that phocids were derived from a lutrine ancestry. The species evidently should be ranked as a very late development in sea otter evolution and one which shows very close affinity to the living species.

The multicusped, left, deciduous P_4 from the Timm's Point Silt (Early Pleistocene), which Mitchell (1966, p. 1909, figs. 4a-c) referred to *Enhydra* cf. *E. lutris*, allows little basis for direct comparison with the permanent dentition of *E. macrodonta*. Mitchell referred the Timm's Point fossil to the living species on the basis of obvious resemblance, but recognized that it differed from the compared specimens of *E. lutris* in being generally larger and in various details of occlusal morphology. The Timm's Point tooth was found to be slightly larger than two lower deciduous fourth premolars of *E. lutris* which were available in the present study (Table 1) and two others examined at the U. S. Geological Survey (Repenning, pers. comm. 1972). The fact that the deciduous tooth from Timm's Point Silt and the permanent premolars and M_1 of *E. macrodonta* are larger than their counterparts in *E. lutris* may be significant and open up the possibility that the Timm's Point fossil may be more closely related to *E. macrodonta* than to *E. lutris*. In addition, if the Late Pleistocene post-cranial elements described by Mitchell are indeed those of *E. lutris*, then it would appear probable that *E. macrodonta* and *E. lutris* coexisted in the northeastern Pacific during some part of the Pleistocene, perhaps as geographically separated populations.

The right M_1 of *E. macrodonta* shows a crude resemblance to the right M_1 of *Lutra reevei* Newton from the Norwich Crag (England) of Middle Pleistocene age, in having the same number and gross arrangement of cusps and ridges. It differs principally in having: 1) about twice the occlusal area; 2) a much squarer occlusal outline with a blunter anterior margin; 3) a paraconid which is proportionately smaller and lies more posterior to the protoconid; and 4) the mesoconid

and metaconid positioned in a relatively more anterior position. These differences, taken in combination, would seem to indicate that *E. macrodonta* and *Lutra reevei* are not particularly closely related and that the M_1 of *L. reevei* was not a suitable morphologic structure for the derivation of M_1 in *E. macrodonta* in the interval from Middle to Late Pleistocene. Thus the author is in accord with Mitchell (1966) and Repenning (1967) that *L. reevei* is not ancestral to *Enhydra*. *Lutra reevei*, on the contrary, seems more closely allied to the Recent *Aonyx capensis* Schinz and the Pliocene *Enhydriodon africanus* Stormer, both from South Africa.

Adaptations: In comparison with *E. lutris* species of the same growth stage, the coronoid process in *E. macrodonta* is consistently shorter with respect to jaw length. This relationship suggests that the skull was not higher than *E. lutris* and may have been slightly lower.

Preserved insertional structures on the mandible of *E. macrodonta*, including those for the masseter, internal pterygoid, and temporal muscles, appear on the whole to be much less strongly formed than their counterparts in *E. lutris*. This circumstance suggests that the jaw musculature of *E. macrodonta* was generally less developed than that of the living species. If this line of reasoning is correct then it remains to be explained why *E. macrodonta* was endowed with substantially larger and heavier posterior teeth than is *E. lutris*. In theory this condition would seem to require that the jaw muscles of *E. macrodonta* would have to be more powerful than those for *E. lutris*, not less, as a comparison of the muscle insertion parts seem to suggest. No satisfactory explanation has been found for this apparent paradox.

It is possible that the musculature of *E. macrodonta* was, indeed, proportionately stronger than that of *E. lutris* but that: 1) the insertional structures do not reflect this condition, or 2) the insertional structures were not yet fully developed in the young adult of *E. macrodonta* and would be larger and more strongly formed in the fully adult state.

Environment of deposition: *Enhydra macrodonta* was recovered from a gray, clayey, fine-grained sand containing the following molluscan species: *Yoldia* sp.; *Mytilus californianus*; *Clinocardium* sp.; *Macoma nasuta*; *Solen sicarius*; *Cryptomya californica*; *Teredo* (?) sp.; *Epitonium indianorum*; *Polinices lewisii*; *Thais lamellosa*; *Thais lima*; *Nassarius fossatus*; *Nassarius rhinetes*; and *Olivella biplicata*. The configuration of topographically higher exposures of Franciscan Forma-

tion rocks (Late Jurassic-Late Cretaceous), north and east of the Crannell Road deposit, indicate that the deposit probably accumulated in a semi-protected marine embayment along an open coast. The fossil assemblage and associated sediment indicate that the site of deposition was a muddy bottom which probably did not exceed five fathoms in depth. Some rocky outcroppings were located nearby.

Age: The recency of the otter-bearing deposit at Crannell Road is suggested by the following lines of evidence: 1) general lack of consolidation of the sediments and near horizontal attitude of bedding; 2) except for *Clinocardium* sp., which may be an extinct species, all the other mollusks in the otter-bearing deposit are presently living along the Humboldt County coast; and 3) fish otoliths found in the gray, pebbly sand, immediately below the otter-bearing unit (see description of the type locality above) are the same as those from the Palos Verdes Sand (Late Pleistocene) of San Pedro (Fitch, 1970).

Mammalian remains from the otter-bearing unit and from a marine deposit at Moonstone Beach, located 1½ miles north of Crannell Road, suggest somewhat greater precision in dating *Enhydra macrodonta*. From the pebbly, fossiliferous sand unit, which stratigraphically underlies the otter-bearing unit, C. A. Repenning (pers. comm. to R. Kohl, 1972) has identified an upper premolar apparently inseparable from the sea lion, *Eumetopias jubata*. Repenning suggests that this tooth, based on limited material from other areas, is no older in age than Rancholabrean (Late Pleistocene). The Moonstone Beach deposit, which appears to contain a marine invertebrate fauna slightly older than that of the otter-bearing unit, has yielded the left scaphoid of a mammoth, *Mammuthus* sp. Repenning (pers. comm. 1972) considers this element to be no older in age than Irvingtonian (Middle Pleistocene), although it may be slightly younger.

Thus the available evidence points to a Rancholabrean or Late Pleistocene age for *Enhydra macrodonta*.

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RESEARCH NOTES

FIRST RECORD OF THE GIANT SEADEVIL *Ceratias holbolli* FROM CALIFORNIA, BASED UPON A SPECIMEN FROM THE STOMACH OF A SPERM WHALE

A giant seadevil *Ceratias holbolli* Krøyer, 1845, the largest of the deep sea anglerfishes, was recovered from the stomach of a 13.0 m male sperm whale *Physeter catodon* that was killed on 13 November 1970, at lat. 37°50'N, long. 123°48'W (115 km west of San Francisco). This position is over the outer edge of the continental slope where the water is about 3,500m deep. The whale was taken by the catcher boat ALLEN CODY, Captain Douglas Campbell, of the Del Monte Fishing Company's whaling station in Richmond, California. Bernard Lenheim, then with the National Marine Fisheries Service (NMFS), examined the stomach of the whale (Field No. 1970-53). Elbert H. Ahlstrom of the NMFS, John E. Fitch of the California Department of Fish and Game, and Robert J. Lavenberg of the Museum of Natural History of Los Angeles County identified the anglerfish, which is deposited in the collection of the latter institute (LACM 31841-1).

Although the giant seadevil is virtually cosmopolitan, it has not previously been collected nearer to California than Cocos Island, the Galapagos Islands, the Hawaiian Islands, and Japan (Clarke, 1950). The few metamorphosed specimens that have been collected were caught at depths of 120 to 4390m, but most catches shallower than 600m were made in Arctic waters (Bertelsen, 1951; Clarke, 1950; Grey, 1956). The species was originally described by Krøyer (1845) on the basis of a specimen collected off Greenland.

This seadevil was the only one that I and my assistants found in the stomachs of 552 sperm whales taken off central California that we examined from 1959 through 1970. Sperm whales are deep divers (they are known to descend as deep as 1,134m) and feed mostly on large squids, but they also eat many large demersal and mesopelagic fishes. *Ceratias holbolli* has previously been reported from the stomachs of sperm whales taken in the Antarctic at lat. 61°S, long. 103°E (Clarke, 1950), off Western Australia (Bannister, 1970), near the Falkland Islands (Korabel'nikov, 1959), off South Africa (Penrith, 1967), and around the Azores (Clarke, 1956).

Although the specimen is partially digested, it is essentially entire and much of its skin is intact; the illicium is present, but the esca is missing. The total length of the fish is about 63cm excluding the caudal rays, which are missing. When whole, it

was probably about 75 or 80cm long. The maximum length reported for this species is 120cm (Bertelsen, 1951). The specimen is doubtless a female; the dwarf males of this species are parasitic on the females.

The vernacular name "giant seadevil" was suggested by Carl L. Hubbs, Scripps Institution of Oceanography, and will be used in a forthcoming check list of California fishes. In the spelling of the specific name and the date of its original publication, I have followed the advice of W. I. Follett, California Academy of Sciences.

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- Accepted for publication May 24, 1972.

**PLIOCERCUS EURYZONUS COPE:
AN ADDITION TO THE SNAKE
FAUNA OF HONDURAS**

Studies in progress on the snake fauna of Honduras revealed the presence of a specimen of *Pliocercus euryzonus* (MCZ 22911) from Tela, Depto. Atlántida, misidentified as *Tropidodipsas sartorii*. This specimen represents the first record of the species from Honduras, even though it is known to occur north and south of this country. The species is now known to inhabit low, moderate, and intermediate elevations along the Atlantic versant from central Guatemala to Brazil (Peters and Orejas-Miranda, Bull. U.S. Nat. Mus., 297:1-347, 1970). It seems likely that the nominal species *Pliocercus annellatus* Taylor, *P. arubricus* Taylor, and *P. dimidiatus* Cope are based on specimens of *Pliocercus euryzonus* (fide Scott, Ph.D. dissertation, Univ. Southern California, 1969, by inference).

The Honduran specimen, a female, has 25 black bands on the body separated by light (red in life?) interspaces one and one-half to two scales in length. The head is black to the middle of the parietals except for a light spot on the first and second supralabials. This black cap is followed by a light nuchal band, which extends to the posterior tip of the parietals. There are 134 ventrals, a divided anal plate, and 1 + 1 temporals, in which features *P. euryzonus* is easily distinguishable from *T. sartorii*, which has over 165 ventrals, a single anal plate, and usually 1 + 2 temporals. The tail of MCZ 22911 is incomplete.

The locality from which this specimen came lies within the Tropical Moist Forest formation or tropical lowland rainforest.

The specimen corresponds to the diagnosis for *P. e. aequalis*; a subspecies which is stated by Stuart (Misc. Publ., Mus. Zool., Univ. Michigan, 122:1-150, 1963) and Peters and Orejas-Miranda (1970) to occur only in central Guatemala. However, it probably ranges south at least to Costa Rica; the specimens upon which the above-mentioned probable synonyms of *P. euryzonus* are based came from this latter country.

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**A NEW SPECIES OF
MICROTROMBICULA
(ACARINA: TROMBICULIDAE)
FROM HIDALGO, MÉXICO**

Studies of the New World *Microtrombicula* Ewing by Vercammen-Grandjean (1965), Webb and Loomis

(1970, 1971a, b, and c), and Loomis and Webb (1971) have resulted in the recognition of three subgenera and 26 species. This new species from Hidalgo, México, tentatively placed in the subgenus *Scapusculata*, is of special interest because of its extremely small size and the absence of certain nude leg setae characteristic of other species of *Microtrombicula*.

***Microtrombicula jacalae*, new species**

Figure 1

Types.—Larvae: Holotype and 21 paratypes from 13 km NE Jacala, 1585 m, Hidalgo, México, from ear of five *Peromyscus boylii levipes* Merriam, original numbers EMF 70-329 (holotype and 4 paratypes), EMF 70-324 (3), EMF 70-325 (1), EMF 70-327 (2).

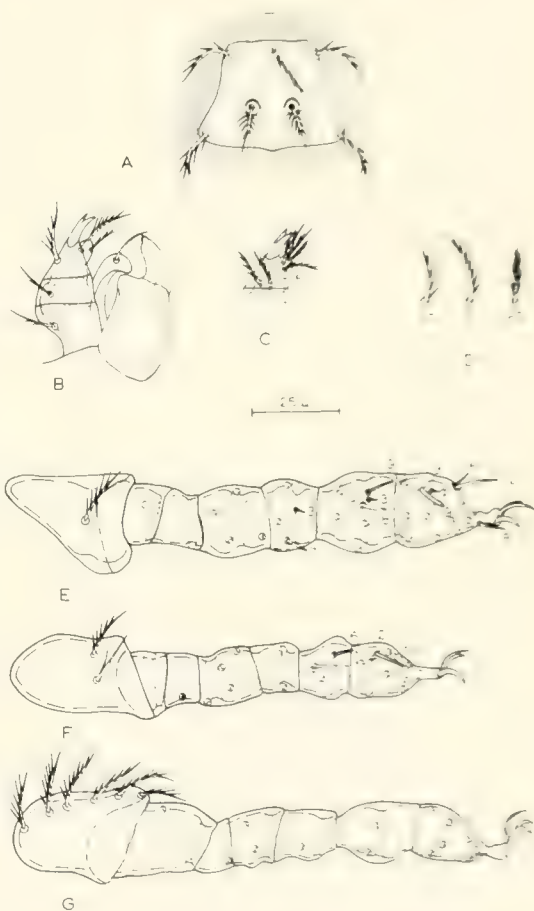


Figure 1. *Microtrombicula jacalae*, new species. A. Scutum. B. Dorsal aspect of gnathosoma. C. Ventral aspect of palpal tibia and tarsus. D. Setae: ST, sternal seta; H, humeral; PD, posterior dorsal. E. Leg I showing nude setae with measurements and measurements of branched setae. F. Leg II, as above. G. Leg III, as above.

and EMF 70-328 (10) taken 30 June 1970, and B69989 (1) from *Peromyscus* sp. taken 2 September 1965, all collected by Eric M. Fisher. The holotype and one paratype will be deposited in the collection of the Rocky Mountain Laboratory, Hamilton, Montana. Other paratypes now in the chigger research collection at California State University, Long Beach will be sent to appropriate institutions.

Diagnosis: Genuae II and III, tibiala III and pretarsala II absent; eyes absent; 1 genua I; coxa III with 5-7 branched setae; coxa II with 2 setae, 1 branched and 1 nearly nude; three pairs of sternal setae; palpotibial claw bifurcate; tarsus III with 13 branched setae (mastitarsala absent); galeala nude.

Description of holotype (measurements in microns, with mean and range of 19 types in parentheses, unless otherwise noted).—Body engorged, 175 by 115; eyes absent.

Dorsal setae 2 (humeral)-6-6-6-4-4, total 28; measurements of humeral seta 17, anterior dorsal seta 19, posterior dorsal seta 22.

Ventral setae 2-2-2 (sternals)-4-2-2-4-4-6-2-2, total 32; measurements of anterior sternal seta 16, anterior ventral seta 15, posterior ventral seta 19.

Scutum: Subpentagonal; sensilla extremely short with 8-10 long setules along shaft.

Scutal measurements: AW 23 (24.3, 22-26; 18), PW 35 (35.5, 32-38), SB 11 (11.2, 10-12), ASB 20 (20.6, 19-23; 18), PSB 13 (13.9, 12-16), AP 25 (24.4, 22-26), AM 16 (15.6, 14-17; 16), AL 14 (14.8, 14-19; 18), PL 22 (20.1, 19-22; 16), S 12 (12.7, 10-15; 7).

Gnathosoma: Cheliceral blade small with small tricuspid cap; cheliceral base and capitular sternum lightly punctate. Galeala nude. Palpal setae B/B/BBB; palpal tarsus with one nude and five branched setae, tarsala 4; palpotibial claw bifurcate with dorsal prong slightly shorter than the recurved ventral prong.

Legs: Segments 7-7-7, extremely short and compressed, each leg ending in 2 claws and clawlike empodium without onychotriches. Leg I with genua 7 and tarsala 9 (8.2, 7-9; 18), pretarsala, subterminala and parasubterminala; leg II with coxa bisetose, 2 tibialae and tarsala 10 (8.9, 8-10), pretarsala absent; leg III with coxa multisetose (5-7 branched setae) and lacking nude setae.

Leg measurements (including, in parentheses, the mean and range of five types): I 36 (125, 116-136); II 114 (107, 92-114); III 131 (130, 117-131); total 381 (358, 325-381).

Taxonomic remarks.—This species is tentatively placed into the subgenus *Scapuscutala*, because of the general similarities to the other species. Also the absence of certain nude leg setae may be correlated with the extremely short leg segments.

The two setae on coxa II also have been recorded for two other species of *Microtrombicula* from West Pakistan (Traub and Nadchatram, 1966) and a larva of *M. trisetica* from Durango, México (Webb and Loomis, 1971c).

Ecological notes.—Of 95 traps set along paths in an oak woodland among or adjacent to limestone outcroppings, five of six trapped *Peromyscus boylii* had *M. jacalae* and a few trombiculid larvae of the genera *Pseudoschoengastia* and *Leptotrombidium*.

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EDITORIAL: CRITICAL REVIEW OF MANUSCRIPTS

As indicated in the Instructions for Authors (inside back cover), all manuscripts submitted to SCAS BULLETIN are reviewed by referees who critically read for scientific content, originality, and clarity of presentation, and who assist the editors in making judgments as to acceptability for publication. The reviewers also assist authors by offering constructive suggestions which may lead to improvement of the text or illustrations of manuscripts. By contribution of their time and professional expertise the referees measurably enhance the quality of SCAS BULLETIN.

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JAMES DALE SMITH, Managing Editor

ANNOUNCEMENT: 1973 ANNUAL MEETINGS

The 1973 annual meetings of the Southern California Academy of Sciences will be held on May 4 and 5, 1973 at California State University, Long Beach. Technical papers are solicited from the fields of natural and social sciences.

Abstracts of no more than 150 words must be typed on 3×5 cards and *must be received no later than March 26, 1973*. The first line of the abstract is to include author(s), student or professional, preferred section (see below), and type of projection equipment, if needed. *Send abstracts to: Donald R. Patten, Natural History Museum of Los Angeles County, Exposition Park, Los Angeles, California 90007.*

Technical sessions—Anthropology, Archaeology, Botany, Earth Science, Entomology, Experimental Biology, Folklore, History, Invertebrate Zoology, Marine Science, and Vertebrate Zoology (other sections will be opened to accommodate demand).

Student awards will be presented in the Natural Science and Social Science Divisions. First award in each division will be \$150.00; second award in each division \$75.00.

A.A.A.S. Grant in Aid of Research—\$150.00 will be awarded to a high school, undergraduate, or graduate student submitting the most outstanding research proposal in the sciences. *Application forms from Takashi Hoshizaki, Department of Biology, U.C.L.A., Los Angeles, California 90024.*

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COVER: *A Little Hermit* (*Phaethornis longuemareus*) hovering above two red spots on the upper surface near the apex of the leaves of *Columnnea florida* (Gesneriaceae). This drawing depicts a proposed new type of hummingbird pollination system involving an extrafloral attraction mechanism in which the attracting unit, in this case the leaf, does not simply simulate a portion of the flower.

Illustration by Susan E. Payne, California State University, Fullerton.

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BULLETIN OF THE SOUTHERN CALIFORNIA
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NUMBER 1

NEW TAXA OF BRACHYURAN CRABS FROM DEEP WATER OFF WESTERN PERU
AND COSTA RICA

JOHN S. GARTH¹

ABSTRACT: Five new species and one new genus of brachyuran crabs obtained by E. M. del Solar and E. Fernandez-B. are described and illustrated. Of these, *Homolodromia robertsi*, *Acanthocarpus delsolari*, *Pilumnus fernandezii*, and *Trizocarcinus peruvianus* are most closely related to western Atlantic deep-water species, whereas, *Delsolaria enriquei*, a new genus and species, is a west American endemic. The family Homolodromiidae and the genera *Homolodromia* and *Acanthocarpus* are reported for the first time from the eastern Pacific. It is postulated that the analogous pairs of deep-water Amphi-american species have been separated since free communication existed at or near the depths at which they presently occur. The Bolivar Trench which extends across northern South America is suggested as the probable Miocene or earlier connection.

Through the efforts of Enrique M. del Solar-C., technical adviser to IMARPE (Instituto del Mar del Perú), carcinological collections from a hitherto untapped source have lately found their way into museums in the United States and western Europe, among them the Allan Hancock Foundation (AHF), Los Angeles, the U.S. National Museum of Natural History (USNM), Washington, and the Royal Netherlands Museum (RNM), Leiden. These come from deep waters off Perú, and are the by-product of a search for edible shrimp and other fisheries products conducted by the research vessels "Wiracocha," "Challua japic," and "SNP-1" under the direction of del Solar. Independent probing of deep waters off western Costa Rica by Hno. Eduardo Fernandez-B., Colegio de La Salle, San José, has similarly enriched the collections of the U.S. National Museum.

Not only have a number of the brachyuran species proven to be new to science, but represented among them are genera and families not previously known to inhabit the eastern Pacific. Four of the new species described herein have already been mentioned in Peruvian journals (del Solar, Blancas, and Mayta, 1970; del Solar, 1972) with identifications to genus only, and three have been illustrated (Chirichigno, 1970), but without specific names. Since the genera under which

they were first reported may differ from the ones used here, and since the published illustrations are sometimes insufficient for species identification, citations to the above are given for clarification only, and are not intended to establish priority for the species in question, which dates solely from this publication. This paper is Allan Hancock Foundation Contribution No. 343.

SYSTEMATIC ACCOUNT

Family HOMOLODROMIIDAE

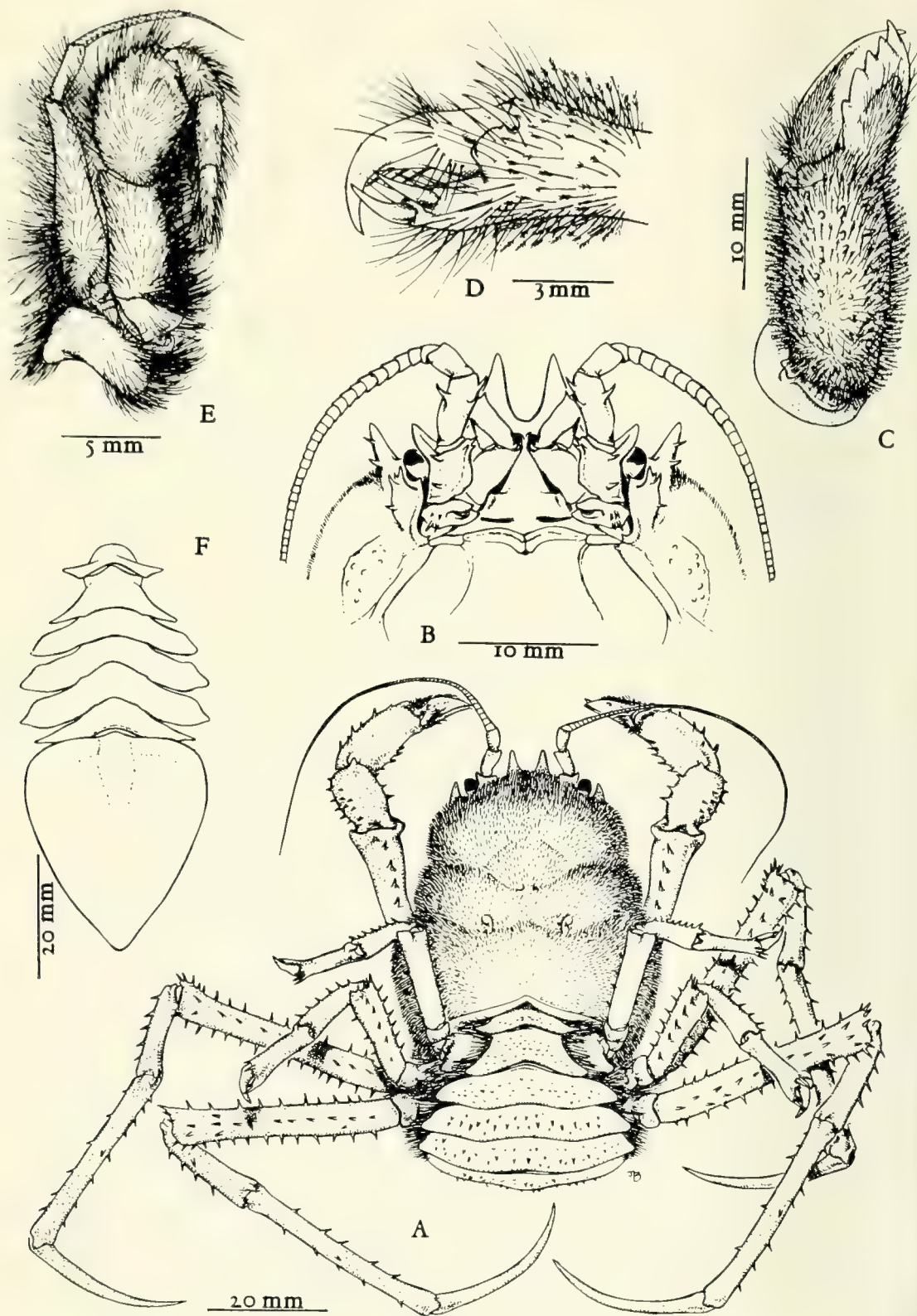
Homolodromia robertsi, new species

Figure 1, A-F

Type: Female, holotype, AHF No. 719, from off Perú, lat. 03°48.5' S, long. 81°18.4' W, 800 m, 11 January 1971, mud bottom, E. M. del Solar, collector (Orig. No. B-260). Ovigerous female, paratype, USNM No. 141570, from off Perú, lat. 07°59' S, long. 80°22' W, 800 m, 26 November 1971, hard bottom, Trawler "Challua japic," E. M. del Solar, collector (Orig. No. B-376).

Measurements (all in millimeters): Female holotype: length, including rostrum, 42.5, width, 38.0, length of rostrum, 4.0, width of rostrum, 7.5, chelipe

¹ Allan Hancock Foundation, University of Southern California, Los Angeles, California 90087



(coxa-ischium-merus, 35.4, carpus-propodus, 37.8), 73.2, chela, 28.0, dactyl, 13.5, height of palm, 7.2, walking legs, from first to last, 98, 90, 36, and 39.

Diagnosis: Rostral and exorbital spines short and subequal, the latter more forwardly than outwardly directed. Median and lateral portions of cervical suture continuous. Carapace, chelipeds, and walking legs spinulous.

Description: Carapace thick, swollen, pilose, surface spinulous, punctate, divided by cervical and branchial sutures into unequal thirds. Posterior branchial regions dilated, limited anteriorly by branchial furrow; anterior branchial regions similarly delimited from gastric and hepatic regions by cervical furrow. Front with two stout, triangular horns reaching extremity of third article of antenna, outer margins sloping toward a similar and forward-directed exorbital spine. Rostral horns and outer orbital spines straight, tubular, the former flattened beneath, the latter spinulous externally. Eyestalks thick, short, cylindrical, two spinules at base; cornea terminal, of diameter equal to eyestalk, color yellowish brown. Supraorbital margin smooth, with a narrow raised border bearing one or two spinules. Lateral margins spinulous, constricted by the aforementioned grooves. Basal antennal article with concealed green-gland opening internally, three or four spinules externally, the outer two in line; second article with two spinules in line externally, a cluster of spinules anterointernally, and a large spine anteroexternally; third (first flagellar) article with a subdistal spinule externally and two spinules in line internally.

Outer maxilliped densely haired, especially along internal margin, merus broader than ischium, arcuate outer margin spinulous; palp coarse, cylindrical.

Chelipeds of female equal, pilose, margins of merus, carpus, and manus spinulous, prehensile margins of fingers dentate, dactylus fitting into a fork-tipped propodus. First two pairs of ambulatory legs long, slender, cylindrical, pilose, spinulous, dactyli long and strongly curved. Last two pairs of legs short, elevated, chelate, chela of third leg directed backward, that of the fourth leg directed forward, dactyl fitting a fork formed by two or more propodal spines.

Female abdomen with seven free segments, seventh segment cordiform, longer than preceding six. The male of the species is unknown.

Remarks: *Homolodromia robertsi* differs from the western Atlantic *Homolodromia paradoxa* A. Milne-Edwards, 1880, as follows: shorter rostral and exorbital spines, the latter more forwardly than outwardly directed; the median portion of

the cervical suture continuous with the lateral portions; the carapace and the walking legs spinulous; and in having the legs of the last two pairs shorter, although this may be a character associated with the female sex. The new species differs from the East African *Homolodromia bouvieri* Doflein, 1904, in having the carapace broader posteriorly, the furrows more clearly discernible, giving it a tightly laced appearance, the rostral and exorbital spines are straight instead of incurving (cf. Doflein, 1904, text-fig. 1), the eyestalks short and thick, the cornea pigmented, the outer maxilliped thicker, the antennal peduncle and walking legs more spinulous, including the meri and propodi, which in *H. bouvieri* are without spinules.

I take pleasure in naming this new species for Henry B. Roberts, Senior Museum Specialist, U.S. National Museum of Natural History, Washington, D.C., whose assistance in preparing its description is gratefully acknowledged.

Family CALAPPIDAE

Acanthocarpus delsolari, new species

Figure 2, A-F

Mursia sp. Chirichigno, 1970, p. 41, text-fig. 85.

Type: Holotype, female, AHF No. 703, from near Banco de Máncora, off Perú, lat. 03°43' S, long. 81°03' W, 250 m, mud bottom, 30 August 1970. E. M. del Solar, collector (Orig. No. B-204).

Measurements (in millimeters): Female holotype: length, 25.3, breadth, 27.6, frontal width, 3.4, fronto-orbital width, 10.8, length of meral spine, 11.0, length of chela, 17.9, dactyl, 7.8, height of palm, 12.1. Overall width, including meral spines, 60.5.

Diagnosis: Carapace ovate, posterolateral spine of moderate length. Two meral spines, the inferior much the longer. Posterolateral margin non-tuberculate. A tooth on posterior margin and a conical tubercle on either side of sternal plastron. Tubercles of carapace arranged in longitudinal rows, most prominent posteriorly and laterally.

Description: Carapace regularly convex, widest opposite middle, surface uneven, protuberances arranged in five longitudinal rows of which one is median, tubercles of lateral ridges increasingly prominent posteriorly, tending to coalesce, the outermost protruding beyond posterolateral margin, which

Figure 1. *Homolodromia robertsi*, new species, female holotype: A. dorsal view; B. ventral view of frontal region; C. outer view of right chela; D. tip of left third walking leg; E. right outer maxilliped; F. abdomen.

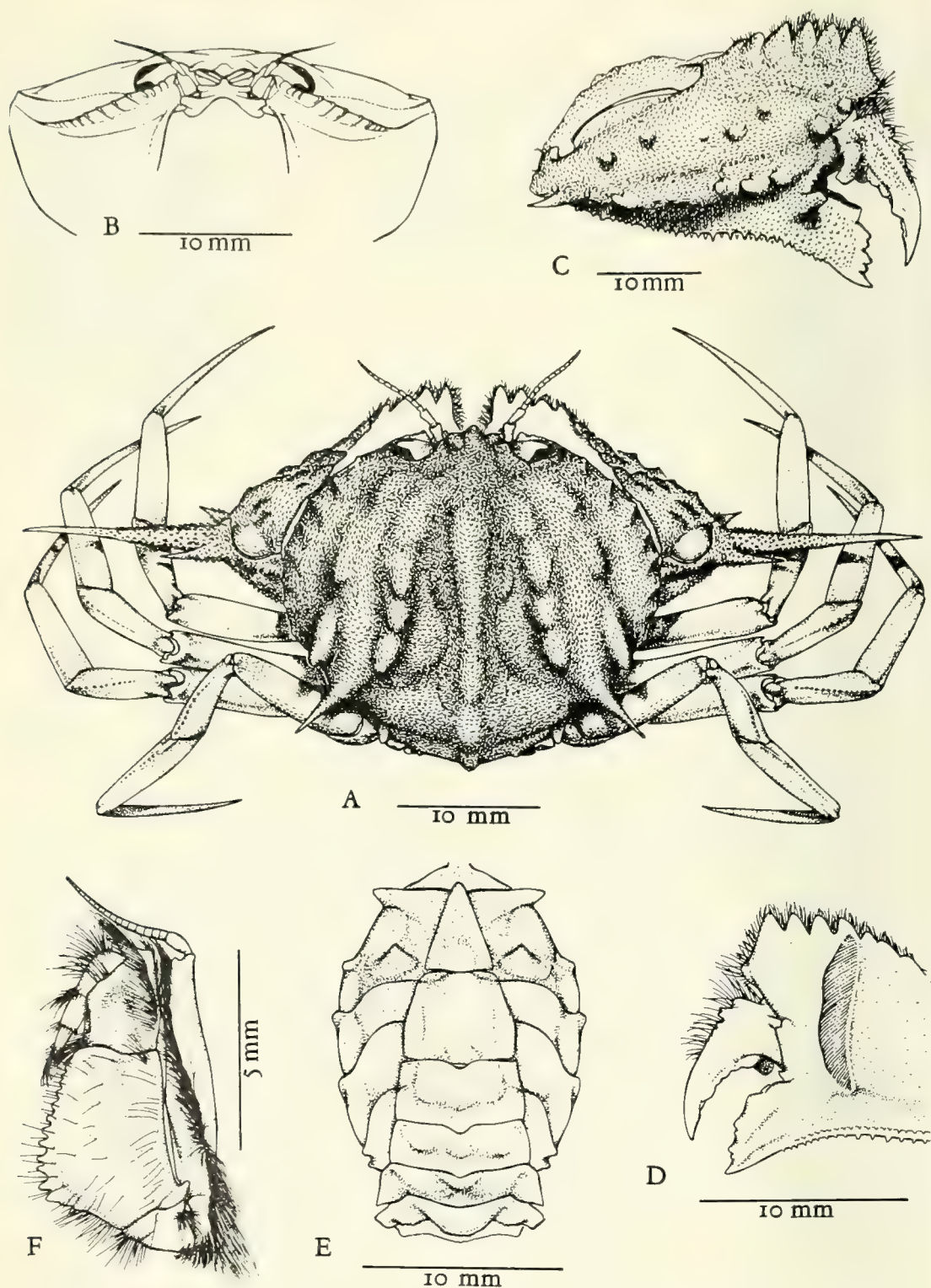


Figure 2. *Acanthocarpus delsolari*, new species, female holotype: A, dorsal view; B, frontal view, showing suborbital tubercles; C, outer view of right cheliped; D, inner view of same, showing stridulating ridge; E, abdomen and sternal plastron; F, left outer maxilliped.

bears a moderately long, conical, more laterally than posteriorly directed spine. Surface covered with minute granules and punctae. Front moderately wide, trilobate, separated from orbit by a shallow notch. Orbits large, margins hairy, superior fissure obsolescent. Anterolateral margin with four obscure tuberculiform teeth, followed by three smaller tubercles at widest part of carapace. Posterior margin arcuate, bearing a large tooth at middle and a smaller tooth on either side.

Spine at outer angle of merus of cheliped approximately two-fifths width of carapace; superior spine approximately one-fifth length of inferior. Hand with a seven-toothed crest above and an oblique, five-toothed crest on outer surface extending from base of dactylus to posteroinferior angle; posterior tooth largest, conical, separated from other teeth by a considerable interval. Six or seven scattered tubercles forming an irregular line between upper and lower crests. Stridulating ridge on inner surface of manus composed of about 47 closely placed, oblique striae, which engage a series of coarser oblique tubercles on the suborbital margin to produce the vibratory grating described for *Acanthocarpus bispinosus* by Rathbun (1937:224).

Outer maxilliped truncate-triangular, inner margin of ischium denticulate, a diagonal row of setae crossing exognath and merus of endognath.

Ambulatory legs naked, unarmed, surface smooth and polished, carpi ridged, propodi laterally compressed, dactyli long, vertically compressed, incurving. A conical tubercle on either side of first sternite.

The male of the species is unknown.

Color in alcohol: Carapace reddish orange, deepest on anterior portion. A spot of orange surrounding each stridulating ridge.

Remarks: The proposed new species appears to be more closely related to *Acanthocarpus alexandri* Stimpson, 1871 (Massachusetts to Windward Islands), type species of the genus, than to *A. bispinosus* A. Milne-Edwards, 1880 (Florida Straits to Windward Islands). *Acanthocarpus delsolari* resembles the former in having the carapace narrowing posteriorly; two meral spines, the inferior the larger; a tooth on the posterior margin; and a pair of tubercles on the sternal plastron. Furthermore, while the postlateral spine is longer than in *alexandri*, it is not as long as in *bispinosus*, nor as laterally directed. *Acanthocarpus delsolari* differs from both in having prominent branchial tuberculate ridges, the outermost actually overhanging the posterolateral margin.

I take pleasure in naming this species for E. M. del Solar, of Lima, Perú, who recognized it as belonging to a genus hitherto unreported from the American west coast.

Family MAJIDAE

Delsolaria, new genus

Type species: Delsolaria enriquei, new species

Description: Carapace ovate-triangular, regions elevated and tuberculated, posterior margin lamellate. Rostrum consisting of two flattened horns. Orbit small, a fissure above and below, the lower one open. Preorbital spine and postorbital cup closely approximated, intercalary spine absent. Basal antennal article broadened basally, forming floor of orbit, a stout spine at anteroexternal angle. Maxilliped with exognath as wide as endognath proximally, ischium widening distally, merus truncate distally, expanded anteroexternally, notched at anterointernal angle. Chelipeds of female slightly more robust than walking legs, manus compressed and carinated, fingers pointed. Walking legs short and stout, carpi tuberculated.

Abdomen of female seven-segmented; male sex unknown.

Relationship: The new genus appears to belong among those genera of the subfamily Pisinae in which the supraocular cave is in close contact with the postocular cup. However, the remarkable broadening of the basal antennal article suggests affinities with certain genera of the subfamily Majinae as well. Final placement and inclusion in a key must await the discovery of a male specimen.

Delsolaria enriquei, new species

Figure 3, A-F

Type: Female, holotype, AHF No. 704, from north side of Banco de Máncora, Perú, 35 m, gravel, 9 December 1970, E. M. del Solar, collector (Orig. No. B-256).

Measurements (in millimeters): Female holotype: length, including rostrum, 37.7, rostrum, 6.2, width at level of branchial spines, 29.6, at level of posterolateral margin, 26.4, cheliped (ischium-merus 12.7, carpus-propodus 17.0), 27.7, chela, 13.8, dactyl, 6.6, height of palm, 4.7.

Diagnosis: Gastric, cardiac, and branchial regions swollen and tuberculate. Lateral branchial tubercle prominent. Rostral, preorbital, and antennal spines of like size and sharpness. Maxilliped distally fringed with clavate setae.

Description: Carapace ovate-triangular, one and one-quarter times longer than wide, highly convex medianly and laterally, elevations studded with rounded tubercles, depressions smooth but microscopically punctate, sides declivitous, posterior margin lamellate. Front bifid, horns sharp, cleft shallow, U-shaped, sides parallel or slightly concave, a double row of curled setae on each: frontal, antennal, and preorbital spines of comparable size and sharpness.

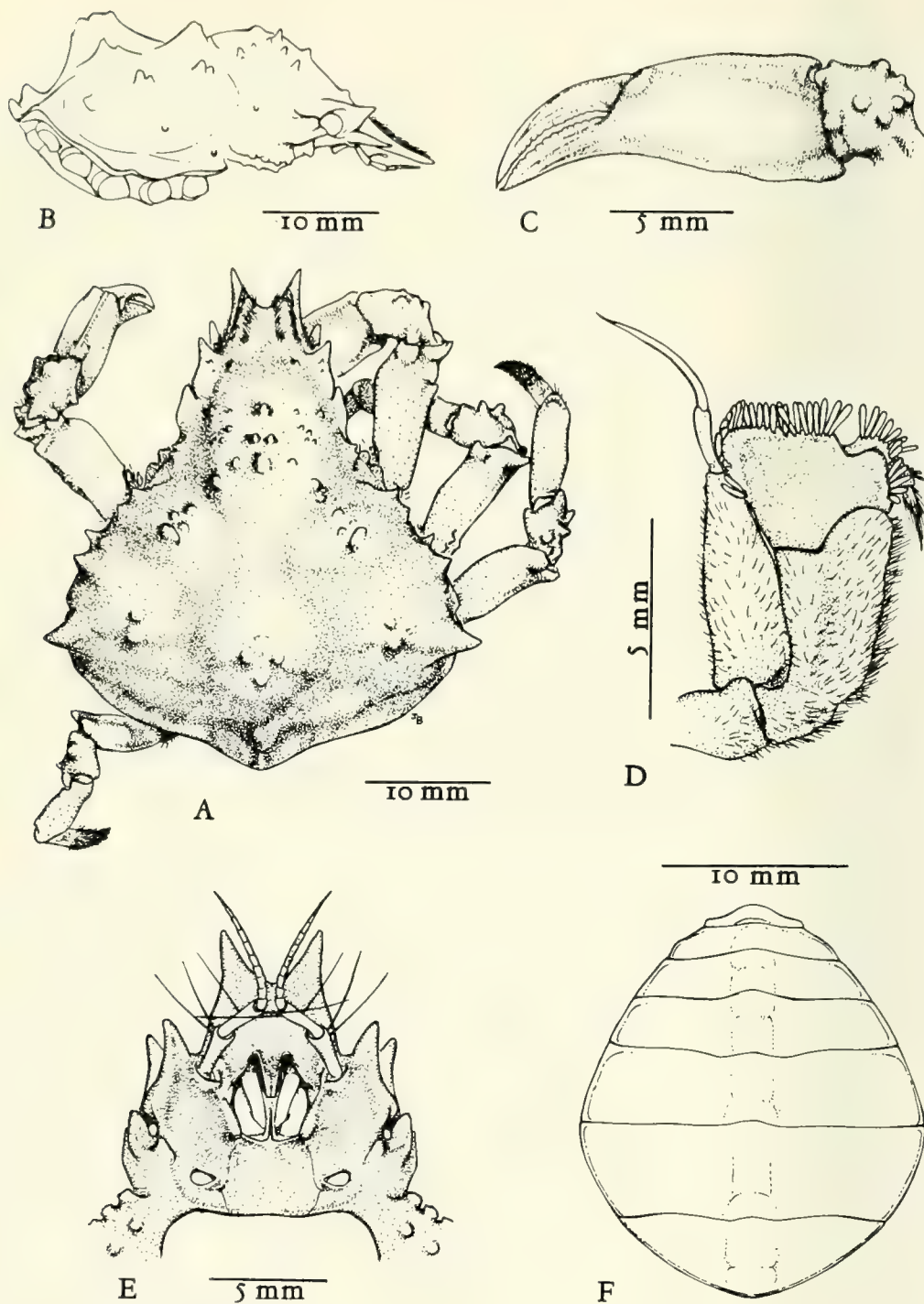


Figure 3. *Delsolaria enriquei*, new species, female holotype: A, dorsal view; B, right lateral view; C, left chela, outer view; D, right outer maxilliped; E, ventral view of frontal region; F, abdomen.

Preorbital spine with outer margin concave, separated by a narrow slit from postorbital cup into which eye retracts, leaving but a fraction of the cornea visible from above, a slight constriction behind postorbital cup. Gastric region broad, swollen, surmounted by a dozen or more small tubercles of which two are median, the others paired; epibranchial regions surmounted by a single large tubercle, with lesser tubercles in advance and on outer slope; mesobranchial regions with three large tubercles forming a triangle, the anterior in line with the lateral and outer epibranchial, the interior in a line with the lateral and anterior cardiac tubercle; cardiac region most elevated, with four tubercles in a diamond with two in line, sides sloping from summit in all directions; sides of hepatic and branchial regions each with one or two small tubercles; intestinal region low, pinched, marked by a single median spine; posterior margin thin, broadly rounded, slightly sinuous, a notch marking off a small lobe at base of second walking leg.

Basal antennal article broad, spine at anteroexternal angle visible from above. Pterygostomial region with a double row of four rounded tubercles.

Exognath of outer maxilliped as broad basally as endognath; ischium of endognath widening distally, invading merus internally, merus broadening anteriorly, expanded externally, and notched internally to receive palpus; distal margins of merus and palpus fringed with clavate setae.

Chelipeds of female slightly more robust than walking legs, merus with anterior and external margins cristate, outer crest with a subterminal spine; carpus tuberculate; manus narrowing distally, crested above and below, fingers long, slender, pointed, downcurving, incurving, ribbed, and multidenticulate.

Walking legs, of which most are missing from the type specimen, short, cylindrical, diminishing in length from first to last, carpi tuberculated, dactyli robust, setose, those of the last pair nearly as long as their propodi, tips incurving.

Female abdomen with seven free segments, each with a low median tubercle.

The male of the species is unknown.

Family XANTHIDAE

Pilumnus fernandezi, new species

Figure 4, A-F

Pilumnus sp. Chirichigno, 1970, p. 55, text-figs. 128, 129.

Type: Male, holotype, USNM No. 141571, Pacific side of Costa Rica, 80 m, E. Fernandez-B., collector (Orig. No. 13). Male, paratype, AHF No. 698, from off Punta Sal, Perú (lat. 03°59' S), 180 m, on continental shelf, 9 May 1969, E. M. del Solar, collector (Orig. No. B-20).

Measurements (in millimeters): Holotype male:

length of carapace, 35.5, width of carapace, including spines, 47.8, length of cheliped (coxa-ischium merus 29.0, carpus-propodus 38.3), 67.3, length of chela, 37.0, of dactyl, 21.0, height of palm, 18.7. Paratype male: length, 29.2, width, including spines, 37.9

Diagnosis: Carapace convex, four anterolateral spines, a subhepatic spine. Three spinules in line inside anterolateral spines. Chelipeds and walking leg spinulous, color of fingers terminating short of palm. Merus of outer maxilliped pentagonal. Tip of first male pleopod doubly recurved.

Description: Carapace one and one-third time broader than long, strongly convex anteroposteriorly, slightly convex from side to side; regions indicated only by a groove outlining the anterior mesogastric, an obtusely angular groove defining the hepatic region, and an H-shaped depression separating the urogastric from the cardiac region; sparsely hairy, with a row of three spinulous granules paralleling the anterolateral margins, and numerous lesser spinules. Front advanced, consisting of two slightly oblique lobes separated by a wide and deep U-shaped sinus, each lobe bearing three spinules; an antennal spinule standing between front and orbit. Orbits broad, spinulous margined, of the spines on upper margin, one next antennal spine and one at about middle, two closed fissures above, three outer lower marginal spines and two inner, the latter on an advanced process bearing two spinules in a longitudinal line on basal portion. Anterolateral spines four, including exorbital spine, each with a conical base and slender tip, inclining successively more outward and upward. Carapace widest opposite fourth spine. Pterygostomial region granulate; a subhepatic spine with a second spinule beneath it. Sternum densely granulate.

Merus of external maxilliped, owing to an inner projection, pentagonal, outer angle rounded, not produced, surface with two shallow depressions, granulate, and hairy.

Chelipeds unequal, the right larger than the left, spinulous, and hairy. Merus with five or six spines along superior margin, the two distalmost largest, curved, and separated by a U-shaped sulcus. Carpus with a prominent inner spine and outer groove as well as spines on upper and outer surface. Manus with two rows of three or four spines above, with lesser spines arranged in rows on outer surface giving way to irregularly arranged spinate tubercles on lower portion. Fingers elongate, meeting with a slight gape, tips crossing; dactyl grooved above, spinulous at base, and with a low bicuspid tooth; pollex deflexed, swollen at base, with a tricuspid tooth followed by a large and a small tooth. Color of fingers terminating in an irregular line considerably short of palm. Minor manus less robust than major, palm completely spinulous, fingers longer and slenderer, teeth thin and triangular, pollex grooved to tip.

Walking legs slender, hairy, longest almost twice the length of carapace, and spinate on anterior margin.

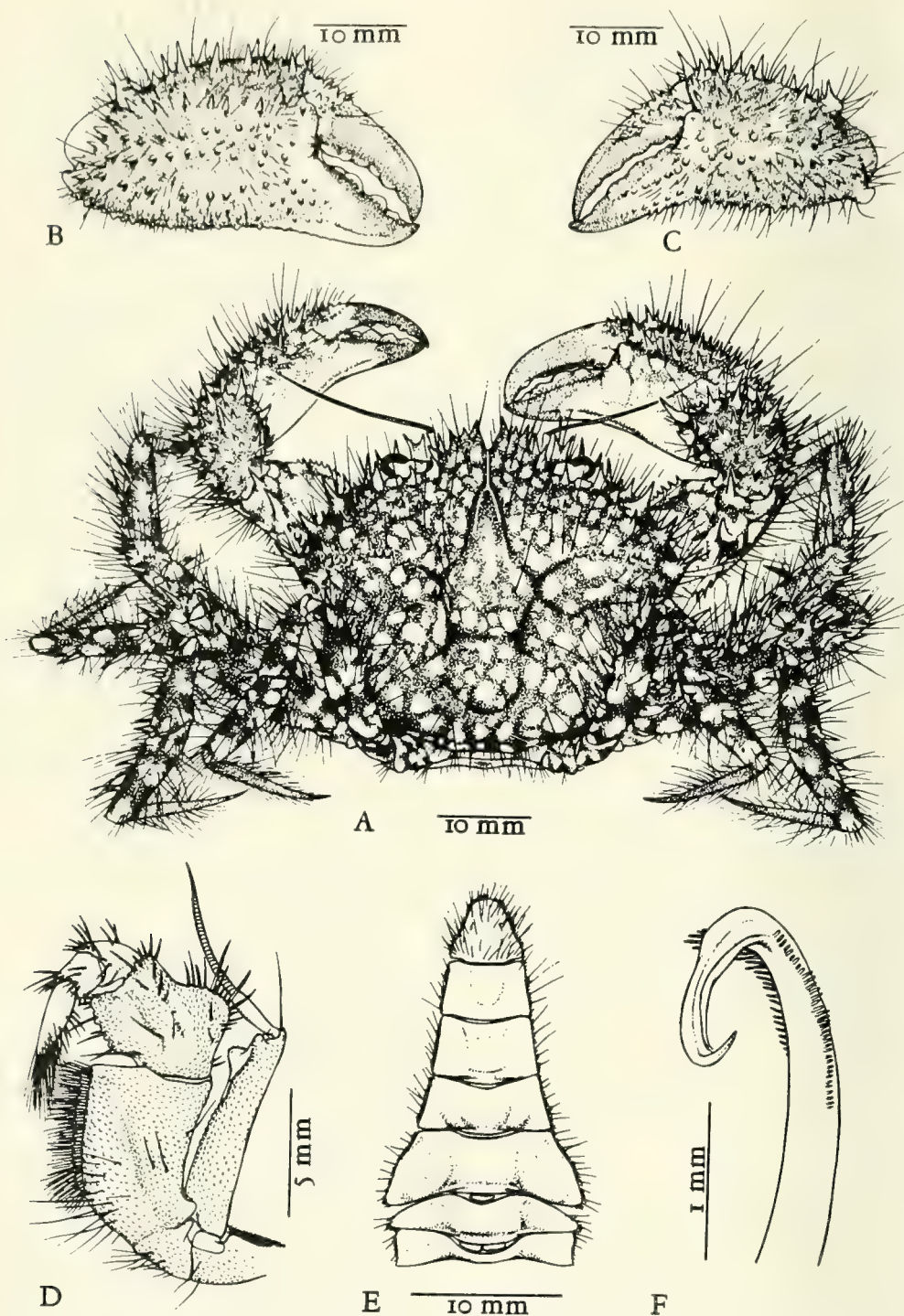


Figure 4. *Pilumnus fernandezi*, new species, male holotype: A, dorsal view; B, right chela, outer view; C, left chela, outer view; D, left third maxilliped; E, abdomen; F, tip of first pleopod.

gins of meri, carpi, and propodi; dactyli long, straight, slightly curved toward tips, nails amber.

Male abdomen smooth-textured with seven segments. The segments beyond third decreasing regularly in width, seventh segment narrowly triangular. Male first pleopod with two rows of marginal setae, tip pointed, sharply recurved.

Color in alcohol: Bright orange-red fading to salmon pink in a network leaving many whitish or cream-colored spots on carapace, chelipeds, and legs; color beneath extending from pterygostomian region onto maxillipeds and sternum. Fingers brown. Hairs golden.

Variation: The paratype from Perú differs from the holotype from Costa Rica in lacking the superior spines on the orbits; these, however, appear to have been broken off on the specimen, which is rigid due to formalin preservation. No trace can be found of the three spinules that parallel the anterolateral margin on the right sides; on the left side the anterior two of these are present but reduced in size. The tips of the fingers of the major chela are worn in the paratype and do not cross as in the holotype specimen. Otherwise, the two compare favorably.

Remarks: I take pleasure in naming this new species for Hno. Eduardo Fernandez-B., Colegio de La Salle, San José, Costa Rica.

Family GONEPLACIDAE

Trizocarcinus peruvianus, new species

Figure 5, A-G

Goneplax sp. Chirichigno, 1970, p. 61, text-fig. 150.

Type: Female, holotype, AHF No. 699, off Paíta, Perú, 80 fathoms (144 m), 10 May 1969, epibenthonic net, E. M. del Solar, collector (Orig. No. B-106). Male, paratype, AHF No. 705, off Perú, depth not stated, 25 February 1970, E. M. del Solar, collector (Orig. No. B-106).

Measurements (in millimeters): Female, holotype: length, 13.1, width, including spines, 19.1, frontal width, 5.5, fronto-orbital width, 16.0, length of right chela, 16.3, of dactyl, 8.7, height of palm, 5.1. Male, paratype: length, 19.9, width, including spines, 28.9, frontal width, 8.2, fronto-orbital width, 22.6, length of right chela, 25.9, of dactyl, 13.5, height of palm, 8.4.

Diagnosis: Only two anterolateral teeth, including exorbital tooth. A sharp transverse ridge opposite lateral tooth. Chelae covered with matted hairs. An infraorbital tooth. No pterygostomian stridulating ridge. Male first pleopod long, straight, attenuated.

Description: Carapace about two-thirds as long as broad, cardiac and posterior branchial regions crossed by a blunt transverse ridge, gastric and anterior branchial regions crossed by a sharper transverse ridge; these ridges dividing carapace into thirds, each inclined at a different plane. Carapace uneven, espe-

cially posterior two-thirds; mesogastric and cardiac regions clearly delimited. Posterior branchial regions swollen, each with a blunt ridge parallel to the converging posterolateral borders. Surface minutely granulate, coarsely punctate, and devoid of hairs. Front bimarginate, upper margin straight, lower margin slightly sinuous, separated from subacute inner orbital angle by a notch. Orbit broad, margin denticulate, two notches above and a closed fissure below the outer tooth; an infraorbital tooth also present. Anterolateral margin with only one tooth behind the flattened exorbital tooth, margin between exorbital and the more slender, cylindrical, and upturned lateral tooth arcuate and denticulate. Ridge on pterygostomian region paralleling epimeral suture blunt, non-striate, and lacking stridulating armature.

Merus of external maxilliped subquadrate, antero-external angle broadly rounded, anterior margin slightly concave, surface matted anteriorly with tomentum.

Chelipeds subequal, the left slightly larger than the right; merus with a sharp spine on upper margin and a dense mat of hairs on internal surface; carpus with a cylindrical tooth on inner margin and a mat of hairs distally; chela with a dense hairy covering externally, leaving only a portion at base of fingers exposed; dactyls slender, elongate, incurving, irregularly dentate, tips crossing.

Ambulatory legs long, slender, carpi and propodi fringed with short hairs, dactyli straight or slightly incurving, with hairy margins.

Male abdomen with seven distinct segments; third segment broadest, like second touching coxae of last pair of walking legs; third to fifth segments concave; base of sixth segment constricted; seventh segment narrowly triangular.

Male first pleopod long, slender, cylindrical, tapering to attenuated tip, and armed with numerous short, conical setae and a few longer setae. Male second pleopod short, curved, tip ovate, concave.

Remarks: *Trizocarcinus peruvianus* differs from *T. tacitus* Chace, 1940, of the western Atlantic by possessing but two anterolateral marginal teeth instead of three, by having the outer surface of the chelae almost completely covered with hairy matting instead of only proximally so, and by having the infraorbital tooth present. Both species differ from *T. dentatus* (Rathbun), 1893, the type species from the Gulf of California, by having the carapace nearly smooth instead of hairy, and by lacking striae on the pterygostomian ridge, which, together with a lamellate ridge on the merus of the cheliped, comprise a stridulating organ in that species. The crisp ridge at the level of the lateral tooth is a further distinguishing feature, although such a ridge is suggested in *T. dentatus*.

The female has been selected as the holotype

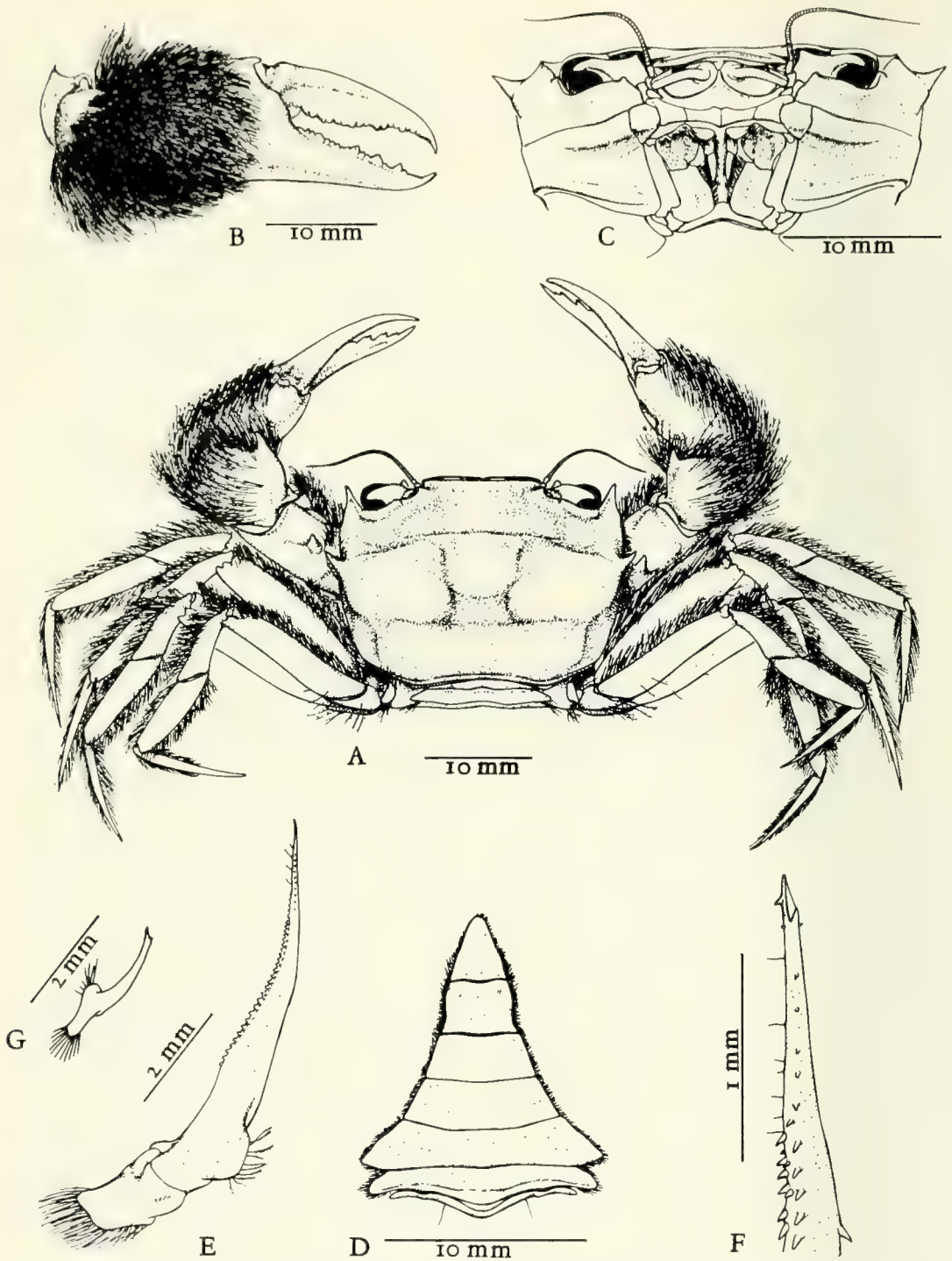


Figure 5. *Trizocarcinus peruvianus*, new species: A–C, female holotype; D–G, male paratype. A, dorsal view; B, outer view of right chela; C, ventral view of front; D, abdomen; E, F, first pleopod; G, second pleopod.

because it has good locality and depth data, both lacking in the male, and is in perfect condition, the male has been dismembered and shows signs of having been dried and rehydrated. The male paratype has been used freely in the description, the male abdomen and gonopod being diagnostic of the species.

DISCUSSION AND CONCLUSIONS

It will have been noted from the foregoing account that the nearest relatives of the newly described eastern Pacific species, where known, are found in the western Atlantic. Thus, the species most closely related to *Homolodromia robertsi* is *H. paradoxa* A. Milne-Edwards, 1880, off Nevis, Leeward Islands, 356 fathoms; the species most closely related to *Acanthocarpus delsolari* is *A. alexandri* Stimpson, 1871, from Massachusetts to the Windward Islands, 45 to 208 fathoms; the species most closely related to *Pilumnus fernandezi* is *P. diomedae* Rathbun, 1894, from the entrance to the Gulf of Mexico, 130 to 184 fathoms; and the species most closely related to *Trizocarcinus peruvianus* is *T. tacitus* Chace, 1940, off Barbados, 209 fathoms. More remarkable still, although this may be an artifact of collecting, with the exception of *Pilumnus fernandezi*, which occurs off Costa Rica, the newly described species have not been found in the Bay of Panama, nor have their Atlantic counterparts been found in the western Caribbean. All are species of the continental shelf and slope, most from below the 100-fathom line, yet not from such abyssal depths as the Peru-Chile Trench (cf. Garth and Haig, 1971) or the Cayman Trench, yet to be explored.

I believe that these deep-water species represent an older and more fundamental relationship between the two faunas than is indicated by the twin or geminate species found intertidally or subtidally on both sides of the Isthmus of Panama. This circumstance is of potentially great significance to marine zoogeographers, who look to evidence of major displacements of marine biotas as confirmation of geological and paleoclimatological changes. Thus, while it is possible that the pelagic larvae of deep-water brachyuran species were able to cross a shallow-water barrier until mid-Pliocene, the date of the last known isthmian closure, the degree of morphological distinctness between their species pairs, which is of a greater magnitude than now exists between the shallow-water species, suggests that effective interchange between the

now-isolated populations ceased long before. Therefore it is postulated that the analogous pairs of deep-water Amphi-american species have been separated since free communication existed between them at or near the depths at which they presently occur. This would date them from Miocene or earlier, when South America was truly an island continent, separated from North America not by a shallow shelf, but by waters of from 100 to 300 fathoms deep. Furthermore, their absence from the Bay of Panama and the western Caribbean would indicate that this deep-water connection was probably not across the present Isthmus of Panama, but across northern South America, perhaps at the Río Atrato-Buenaventura, Colombia, level of the Bolivar Trench.

The one new species that does not appear to fit into this category, and for which it has been necessary to erect a new genus, is *Delsolaria enriquei*. The family Majidae, to which it belongs, is of New World origin, with most of its numerous genera common to the east and west coasts of the Americas, and with parallel speciation on the two sides. There are several endemic west-coast genera, among them *Loxorhynchus* Stimpson, 1857, and *Mimulus* Stimpson, 1860, of western North America, and *Pisoides* A. Milne-Edwards and Lucas, 1843, and *Lophorochinia* (Garth, 1969) of western South America. These are either north or south temperate in distribution, and do not cross the Equator. *Delsolaria* may be placed provisionally in the latter category until its extra-Peruvian distribution becomes known.

ACKNOWLEDGMENTS

I am indebted to Henry B. Roberts, U.S. National Museum of Natural History, Washington, for permission to describe and illustrate *Pilumnus fernandezi*, to Fenner A. Chace, Jr., U.S. National Museum, whose description of *Trizocarcinus tacitus* was followed in describing *T. peruvianus*, and to Danièle Guinot, Paris Museum, whose studies on the Goneplacidae (Guinot, 1969) facilitated its generic placement. The manuscript was read in part (the Majidae) by D. J. G. Griffin, Australian Museum, Sydney, and in its entirety by Henry B. Roberts and by my associate, Janet Haig. A subvention from the Sociedad Nacional de Pesquería of Lima, Perú, provided for the illustrations by Jerry J. Battagliotti.

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A NEW SPECIES OF GERBIL FROM SOUTH WEST AFRICA
WITH REMARKS ON *GERBILLUS TYTONIS* BAUER AND NIETHAMMER, 1959
(RODENTIA: GERBILLINAE)

DUANE A. SCHLITTER¹

ABSTRACT: A new species of *Gerbillus* (*Gerbillurus*) is described from Gobabeb, South West Africa. This new species exhibits the maximum cranial size and bulla hypertrophy known for the subgenus. The skins of *Gerbillus tytonis* are described for the first time. *Gerbillus tytonis* was known previously only by cranial elements taken from owl pellets.

The Smithsonian Institution's African Mammal Project had field parties collect small mammals and their ectoparasites in southern Africa from 1963 until 1969. Among the specimens collected were numerous *Gerbillus*. In southern Africa, this genus is presently in a confusing taxonomic state. There appear to be two groups of nominal species in the genus *Gerbillus* in southern Africa; a "paeba" group including the names listed under *Gerbillus paeba* by Roberts (1951) and subsequent authors and a "vallinus" group including *Gerbillus vallinus* Thomas, 1918, and *Gerbillus tytonis* Bauer and Niethammer, 1959. These species have been included under the subgenus *Gerbillurus* Shortridge, 1942.

Shortridge (1942:52) proposed the name *Gerbillurus* as a subgenus of *Gerbillus* to include only the species *vallinus*. In the original description, *Gerbillurus* was characterized as having a long and relatively tufted tail, which in some examples is half as long again as the head and body, partially bare soles, and a triangular skull with inflated bullae. Although elevated to generic rank by Roberts, 1951, and Lundholm, 1955, *Gerbillurus* was retained as a subgenus of *Gerbillus* by Ellerman, Morrison-Scott, and Hayman, 1953, and the species *vallinus* was included in the genus *Gerbillus* by Meester, Davis, and Coetzee, 1964. Herold and Niethammer (1963:54, 56) concluded that *Gerbillurus* was more closely related to *Tatera* after comparisons of the enamel patterns of the lower first molars of young animals and the molar alveoli of different genera of gerbillines. They did not state conclusively, however, whether *Gerbillurus* should be recognized as a distinct genus or remain as a subgenus of *Gerbillus*.

A review of the taxonomic status of *Gerbillurus* Shortridge, 1942, and the species in both the "paeba" and the "vallinus" groups is underway.

However, this preliminary paper was completed so that the new name would be available.

A new species is being proposed in the "vallinus" group and the skins of *Gerbillus* (*Gerbillurus*) *tytonis* Bauer and Niethammer, 1959, are described for the first time.

METHODS

All measurements were taken with dial calipers and are in millimeters, weights are in grams and capitalized color terms are from Ridgway "Color Standards and Color Nomenclature" 1912. Hind foot measurements of specimens in the Smithsonian Institution include toenail. Total length and length of tail were taken on dorsal surface of specimens; the latter measurement with tail held perpendicular to body. Breadth of auditory bulla is the distance from the outside edge of the auditory meatus to the inner edge of the bulla. All specimens are deposited in the National Museum of Natural History, Smithsonian Institution (USNM), unless otherwise indicated. Specimens from the Transvaal Museum (TM), Pretoria; British Museum (Natural History) (BM), London; and the American Museum of Natural History (AMNH), New York, were also examined. The new species may be known as:

Gerbillus (*Gerbillurus*) *setzeri*, new species

Figure 1

Holotype:—Young adult female, skin and skull. United States National Museum of Natural History

¹ African Mammal Project, Smithsonian Institution, Washington, D.C. 20560 and Dept. Zoology, University of Maryland, College Park 20742.

no. 342253, from 1 mi E Namib Desert Research Station, Gobabeb, South West Africa; obtained 22 November 1963 by A. C. Rissler, original no. 359.

Specimens examined.—Seventy-four, as follows: South West Africa: 1 mi E Namib Desert Research Station, Gobabeb, 23; 8 mi E Namib Desert Research Station, Gobabeb, 1; Namib Desert Research Station, Gobabeb, 10 (1 TM); Swartbank [= Zwartbank] Mountain, 36 km WNW Gobabeb, 22; Tumas Mountain, 1; near Swakopmund, 2 (AMNH); Goanikontes, 3 (AMNH); 10 km E Hope Mine, 1 (TM); east of Gobabeb, 1 (TM); 8 mi E Hope Mine, 3 (TM); east of Hope Mine, 2 (TM); Swakopmund, 5 (TM).

GAZETTEER

Goanikontes	22° 40' S, 14° 50' E
Gobabeb	23° 34' S, 15° 03' E
Hope Mine	23° 34' S, 15° 15' E
Sossus Vlei	24° 44' S, 15° 18' E
Zwartbank Mtn.	23° 22' S, 14° 58' E
Swakopmund	22° 41' S, 14° 32' E
Tumas Mtn.	23° 29' S, 15° 31' E

Measurements.—Selected external and cranial measurements of the holotype are: Total length, 249; length of tail, 143; length of hind foot, 32; length of ear from notch, 15; occipitonasal length, 32.6; greatest breadth across zygomatic arches, 17.1; greatest breadth of braincase, 15.1; height of skull, 13.5; least interorbital breadth, 5.3; length of nasals, 12.8; oblique length of audital portion of auditory bulla, 11.8; crown length of maxillary toothrow, 4.5; greatest breadth of M^3 – M^3 , 5.1; length of anterior palatine foramina, 5.7; and length of posterior palatine foramina, 25. Comparative measurements of three species of *Gerbillus* (*Gerbillurus*) are given in table 1.

Diagnosis.—Upper parts near Light Pinkish Cinnamon, with slight admixture of gray hairs; all hairs plumbeous at base. Circumoral, entire underparts, supraorbital and postauricular spots, and dorsal surfaces of hands and feet, white; all hairs uniformly white to base. Sharp line of demarcation present between dorsal and ventral colors of body. Tail relatively short for subgenus and bicolored, dorsal color same as color of back, ventral color white; tail with penicillate tip of Mouse Gray dorsal hairs on distal one-third. Color of back extending to hairs on external surface of pinna; hairs of internal face of pinna white; flesh of pinna Cinnamon-Buff. Skull large for subgenus; upper toothrow relatively short and robust; audital and mastoidal portions of auditory bulla relatively large and well inflated ventrally and posteriorly; mastoidal portion of auditory bulla projecting beyond occiput; external auditory meatus well inflated anteriorly and foramen of Huschke well developed ventrally; anterior palatine foramina relatively short and wide; posterior palatine foramina long.

Comparisons.—From the nominal species of

the *Gerbillus paeba* group in southern Africa, *Gerbillus* (*Gerbillurus*) *setzeri* can be distinguished by its larger size, both externally and cranially. The large size of the body and the hind feet serve at once to distinguish this new species from any of the smaller *G. paeba*.

From *Gerbillus* (*Gerbillurus*) *vallinus vallinus* as known from the vicinity of Berseba, South West Africa, and Tuin, South Africa, this new species differs externally by having a shorter tail, longer hind feet, smaller ears and being dorsally paler in color. Cranially, the skull of *G. setzeri* is longer and broader, the bulla larger and more inflated, the breadth across M^3 – M^3 narrower, and the least interorbital breadth narrower than *G. v. vallinus*.

Gerbillus setzeri differs from representatives of *G. vallinus seeheimi* from Seeheim, South West Africa, and numerous localities in the northern Cape Province, South Africa, by the lack of black hairs that are suffused in the dorsal pelage and make up the tufted tip of the tail in *G. v. seeheimi*. Skulls of *G. setzeri* differ from *G. v. seeheimi* in the same manner as from the nominate subspecies. Even though the breadth across M^3 – M^3 is less in *G. v. seeheimi* [5.1 (4.7–5.4) 25] than in *G. v. vallinus* [6.3 (6.1–6.5) 7], this distance is still greater than the same measurement in *G. setzeri* (Table 1).

Representatives of *Gerbillus tytonis* taken at the type locality of *G. setzeri* can be distinguished by the smaller size of the body, shorter and narrower skull, less inflated auditory bulla, and markedly shorter posterior palatine foramina. The dorsal pelage of *G. tytonis* is darker in color than that of *G. setzeri*; the former is a reddish gold color and matches the red sand of the desert south of the Kuiseb River at Gobabeb whereas the latter is a paler color near Light Pinkish Cinnamon and more nearly matches the pale feldspar and quartz plains north and east of the Kuiseb River at Gobabeb.

Statistical Analysis.—Initially, samples of males and females of each of the three species were compared to determine if any secondary sexual variation existed in mensural data. Weights were not included in these tests. These analyses revealed the absence of secondary sexual variation in all of the measurements tested in each of the three species; consequently the sexes were combined for subsequent tests of significant differences between the species. In addition, comparisons between *Gerbillus vallinus vallinus* and *G. v. seeheimi* revealed these two subspecies were sig-

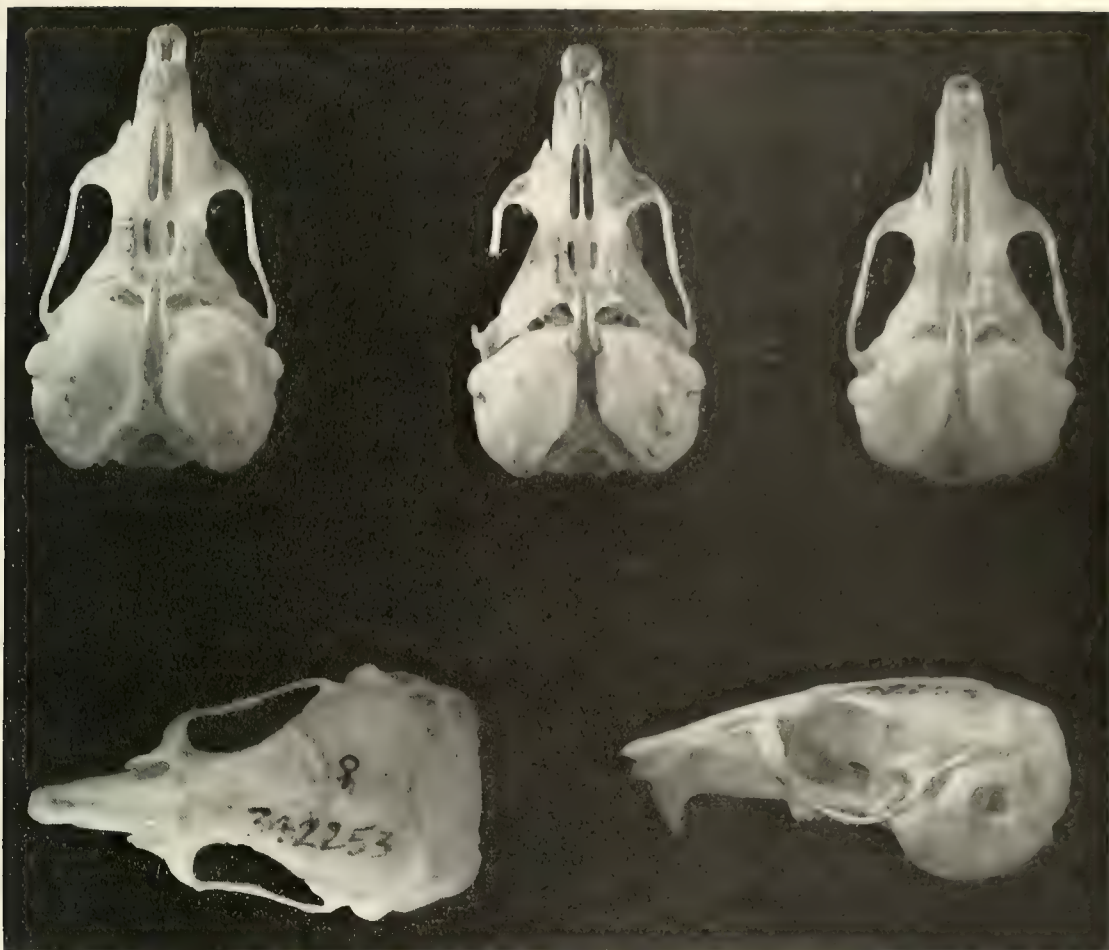


Figure 1. Skulls of the three species of the *Gerbillus vallinus* group. Top row, ventral views from left to right: *Gerbillus setzeri* holotype (USNM 342253); *G. vallinus vallinus*, Berseba, South West Africa (USNM 304852); and *G. tytonis*, Namib Desert Research Station, Gobabeb, South West Africa (USNM 342196). Bottom row, left to right: dorsal view of holotype of *G. setzeri* and lateral view of same skull. (Scale 2 $\times$)

nificantly different only in the breadth across the third upper molars.

Results of statistical comparisons between samples of *Gerbillus setzeri* with samples of *G. vallinus* and *G. tytonis* are given in table 1. Both "t" tests and "F" tests were computed but SS-STP tests were not run inasmuch as only grouped single samples for each species were available. For all but one measurement, the coefficient of variation was within the range considered normal for small mammals. In the case of the posterior palatine foramina, the high values of the coefficient of variation are a result of the difficulty of taking the measurement. Use of an ocular micrometer or a craniometer would undoubtedly

result in lower coefficient of variation values. The high value of the coefficient of variation for the breadth across third upper molars of *G. vallinus* is a result of combining the samples of the two subspecies.

Two of the results of the "F" test are questionably significant. In the comparison of length of ear between *Gerbillus setzeri* and *G. vallinus*, the "F" test would indicate the variances of the two samples are significantly different at the 95 per cent level but the low "t" value (3.189) indicates a questionable difference. In the case of the comparison of crown length of maxillary toothrow between *G. setzeri* and *G. tytonis*, the low "t" value (2.981) again indicates a questionable dif-

TABLE 1. Variation between samples of *Gerbillus setzeri*, *G. vullinus*, and *G. tytonis* from southern Africa. The first line for each measurement includes the mean plus and minus two standard errors, the second line the coefficient of variation and the number of specimens in the sample. Measurements are indicated in which differences between the samples of *G. setzeri* and those of *G. vullinus* and *G. tytonis* are significant (for "t" test, * = 0.05 level of confidence and ** = 0.01 level of confidence; for "F" test, + = 0.05 level of confidence and ++ = 0.01 level of confidence). Abbreviations of measurements are as follows: TL, total length; TA, length of tail; HT, length of hind foot; EN, length of ear from notch; OCN, occipitonasal length; BZA, breadth across zygomatic arches; GBB, greatest breadth of braincase; LIB, least interorbital breadth; GBR, breadth of rostrum; GLN, greatest length of nasals; LAB, oblique length of auditory bulla; CLT, crown length of maxillary toothrow; BPM, breadth of palate at M¹; LPF, length of anterior palatine foramina; PPF, length of posterior palatine foramina; GHS, greatest height of skull; and GBW, breadth of auditory bulla.

	<i>G. setzeri</i>	<i>G. vullinus</i>	<i>G. tytonis</i>	<i>G. setzeri</i>	<i>G. vullinus</i>	<i>G. tytonis</i>
TL	233.02 ± 2.836 (217-263) 4.13 43	239.85 ± 4.540* (215-266) 4.83 26	225.71 ± 2.260** (205-240) 3.71 55	GLN 12.29 ± 0.172 (11.4-13.1) 3.76 29	11.34 ± 0.184** (10.3-12.4) 4.73 34	11.62 ± 0.161** (10.5-13.0) 5.12 55
TA	127.35 ± 1.979 (113-145) 5.09 43	138.85 ± 3.871** (119-156) 7.11 26	126.49 ± 1.698 (113-141) 4.98 55	LAB 11.39 ± 0.116 (10.6-12.4) 3.01 35	10.62 ± 0.091** (9.9-11.0) 2.50 34	9.80 ± 0.068**+ (9.3-10.4) 2.36 47
HT	32.45 ± 0.365 (30-35) 3.73 44	31.19 ± 0.414** (30-34) 3.45 27	33.37 ± 0.377** (28-36) 4.26 57	CLT 4.33 ± 0.075 (4.1-4.6) 3.77 19	4.08 ± 0.072** (3.7-4.5) 5.08 33	4.23 ± 0.033***+ (4.0-4.5) 2.78 50
EN	13.86 ± 0.254 (12-16) 6.01 43	14.44 ± 0.222**+ (14-16) 4.00 27	12.96 ± 0.180** (12-14) 5.25 57	BPM 5.07 ± 0.055 (4.9-5.3) 2.47 7	5.37 ± 0.189 (4.7-6.5) 9.97 32	4.87 ± 0.065* (4.5-5.3) 4.11 38
OCN	31.43 ± 0.331 (29.5-32.6) 2.52 23	29.90 ± 0.283** (28.2-31.9) 2.64 31	29.34 ± 0.253** (28.1-30.4) 2.82 43	LPF 5.47 ± 0.085 (5.0-6.1) 4.55 34	5.19 ± 0.078** (4.7-5.7) 4.41 34	5.43 ± 0.070 (5.1-6.3) 4.85 56
BZA	16.62 ± 0.153 (15.7-17.4) 2.48 29	15.68 ± 0.155** (15.1-16.8) 2.80 32	15.61 ± 0.183** (14.2-16.6) 3.65 39	PPF 2.32 ± 0.067 (1.8-2.7) 8.73 36	1.98 ± 0.078** (1.4-2.5) 11.45 34	1.08 ± 0.057** (0.6-1.6) 19.87 57
GBB	14.92 ± 0.149 (14.1-16.1) 2.78 31	14.22 ± 0.158** (13.0-15.0) 2.99 29	13.94 ± 0.089***+ (13.4-14.6) 2.10 43	GHS 13.20 ± 0.118 (12.7-13.8) 2.10 22	12.68 ± 0.137** (11.9-13.2) 2.70 25	12.44 ± 0.090** (12.0-12.8) 1.94 29
LIB	5.56 ± 0.053 (5.3-5.9) 2.83 35	5.75 ± 0.076 (5.4-6.3) 3.86 34	5.51 ± 0.048 (5.2-6.0) 3.29 57	GBW 9.04 ± 0.111 (8.1-9.7) 3.63 35	8.61 ± 0.082***+ (8.0-9.0) 2.78 34	8.34 ± 0.060***+ (7.9-8.9) 2.53 49
GBR	4.07 ± 0.054 (3.6-4.3) 3.80 33	3.94 ± 0.075** (3.5-4.2) 5.46 33	4.11 ± 0.044 (3.7-4.5) 4.04 56			

ference between the variances of the two samples. In all other instances where the "F" test is significant, "t" values are high (6.181–25.003).

Remarks.—*Gerbillus setzeri* is apparently restricted to the very pale feldspar and quartz gravel plains in the Namib Desert. In sharp contrast to this distribution is that of *Gerbillus tytonis*, a species apparently found only on the shifting red sands south of the Kuiseb River. In November of 1963, field collectors for the Smithsonian Institution took both species at Gobabeb in the red sands of the dry river bed and adjacent dunes south and west of the research station. At this time both species were rather common in the vicinity of the field station. According to the late Charles Koch (pers. comm., 1969) in March of 1963, unusually heavy rains fell in the vicinity of Gobabeb and the area to the west with subsequent heavy flooding in the Kuiseb River. In the months following these rains, vegetative growth on the gravel plains was exceptionally lush according to Dr. Koch. Judging from the ages of the specimens taken by the field collectors, by November a good breeding season had been experienced inasmuch as mostly juveniles, subadults and young adults were trapped. No old adults were included in either of the samples of *G. setzeri* from Gobabeb or downstream near Zwartbank Mountain, also situated on the bank of the Kuiseb River. During this period of higher population levels, individuals of *Gerbillus setzeri* apparently dispersed from the gravel plain across the river bed and into the adjacent red sand dunes to the south and west of Gobabeb. Extensive trapping at Gobabeb in December 1969 revealed *Gerbillus setzeri* to be found rarely (five specimens in about 400 trap nights) and only on the gravel plain, whereas *Gerbillus tytonis* was commoner but found only on the red sands. Individuals of the *Gerbillus paeba* group were found ubiquitously distributed and common at Gobabeb in 1969.

The single individual from Tumas Mountain was taken in fine sand with less gravel present; dry grass formed a rather uniform cover in this area. The locality 10 mi E Hope Mine was also visited and proved to be nearly identical to the gravel plains near Gobabeb and Zwartbank Mountain. Meester (1963:245) reported a male specimen shot on the gravel plain east of Gobabeb.

In the only sample of weights available for *G. setzeri*, males averaged heavier than females taken at Zwartbank Mountain. Eight adult males

averaged 39.5 (37.0–42.5); whereas nine adult females averaged 34.3 (29.5–39.0).

Meester (1963:245) reported an individual from east of Gobabeb as *Gerbillus vullinus vullinus*. A skin with broken skull in the Transvaal Museum (TM 12929) was taken east of Gobabeb by the Bernard Carp expedition. This specimen is probably the same one reported by Meester and is referred here to *G. setzeri*.

This new species is named after Dr. Henry W. Setzer in honor of his efforts in African mammalogy and in particular for his interest in the taxonomy of desert rodents.

REMARKS ON *GERBILLUS* (*GERBILLURUS*) *TYTONIS* BAUER AND NIETHAMMER, 1959

Originally proposed by Bauer and Niethammer (1959:255) as a subspecies of *Gerbillus vullinus*, *Gerbillus tytonis* was described from a collection of skulls removed from owl pellets collected at Sossus Vlei, South West Africa. Davis (1968:4) regarded *G. tytonis* as worthy of specific status; he distinguished *tytonis* from *vullinus* by the very short posterior palatine foramina and the small bullae of *tytonis*. I concur with this separation of *G. tytonis* from *vullinus*. In spite of the large amount of variation present in the length of the posterior palatine foramina of *G. tytonis*, this measurement is still significantly shorter than that of *G. vullinus*. *Gerbillus tytonis* is the smallest species of the "vullinus" group (Table 1).

To my knowledge, *G. tytonis* is known in the literature only from skulls recovered from owl pellets; a description of the skins of this species based on adult specimens taken on 28 March 1966 at the type locality follows:

Upper parts near Hazel; all hairs plumbeous at base. Entire underparts, small supraorbital and well-defined postauricular spots, and dorsal surfaces of hands and feet, white; all hairs uniformly white to base. Sharp line of demarcation present between dorsal and ventral color of pelage. Tail relatively long for subgenus and bicolored, dorsal color same as color of back, ventral color same as dorsal but with admixture of white hairs; tail with variable penicillate tip of grayish hairs. White circumoral ring absent. Ears essentially bare and Cinnamon-Buff in color; narrow fringe of black pigmentation present on lateral margin of pinnae.

The dark dorsal pelage, long feet, small size of

body and skull, short posterior palatine foramina and small bullae serve to distinguish *Gerbillus tytonis* from *G. vallinus*.

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Others who deserve thanks for helping make this paper possible are, obviously, the many persons who collected mammals for the Smithsonian Institution in southern Africa. In addition, a special debt of gratitude is owed J. A. J. Meester, University of Natal, Pietermaritzburg; D. H. S. Davis, formerly with South African Medical Ecology Centre, Johannesburg; the late Dr. C. Koch and I. L. Rautenback, Transvaal Museum, Pretoria; and C. G. Coetzee, State Museum, Windhoek, for their efforts and suggestions. Staff photographers at the National Museum of Natural History made the skull photographs and Mrs. Helen J. Hutchinson typed the manuscript.

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POLYCHAETES FROM CENTRAL AMERICAN SANDY BEACHES

KRISTIAN FAUCHALD¹

ABSTRACT: Twenty-six species of polychaetes are reported from sandy beaches in Colombia, Panama, and Costa Rica from the Atlantic and Pacific Oceans. Two new species and one new genus are described.

The polychaete fauna of Central America has been the subject of several studies; early literature was summarized by Monro (1928, 1933a, 1933b). Hartmann-Schroder (1959) described polychaetes in shallow-water quantitative samples from mangrove areas of El Salvador. Sandy beaches, however, have been largely neglected until recently.

The present collections were made under the supervision of Deborah M. Dexter of California State University, San Diego, over a period of two years for the purpose of comparing the total fauna of the sandy beaches of the Atlantic and Pacific Oceans of Central America.

STATION LIST

Several beaches were collected at different times, so the list contains location only. Because of the complex coastlines, the stations are listed alphabetically within each country.

ATLANTIC OCEAN

Colombia:

Boca Grande, Cartagena, 10°30' N, 75°40' W
Isla San Andres, 12°32' N, 81°34' W
Pradomar Beach, Puerto Colombia, 11°08' N, 75°09' W
Rodadero Beach, Santa Marta, 11°15' N, 74°13' W

Costa Rica:

Airport Beach, Limon, 9°58' N, 83°01' W
Cahuita North, 9°45' N, 82°52' W
Cahuita South, 9°44' N, 82°50' W
Playa Bonita, Limon, 10°01' N, 83°04' W
Puerto Viejo, 9°40' N, 82°44' W

Panama:

Pina Beach, 9°20' N, 80°05' W
San Blas, 9°30' N, 79°20' W
Shimmey Beach, 9°23' N, 79°57' W

PACIFIC OCEAN

Colombia:

Playa Juan Chaco, N of Buenaventura, 4°10' N, 77°30' W

Costa Rica:

Boca de Barranca, Puntarenas, 9°58' N, 84°45' W

Jaco, 9°37' N, 84°38' W
La Punta, Puntarenas, 9°59' N, 84°52' W
Playa Cocal, Quepos, 9°26' N, 84°10' W
Playa Espadilla, Quepos, 9°24' N, 84°10' W
Playita Blanca, Playas del Coco, Coco, 10°34' N, 85°42' W
Samara, 9°53' N, 85°38' W
Tamarindo, 10°19' N, 85°50' W
Panama:
Naos Island, 8°53' N, 79°33' W
San Carlos, 8°29' N, 79°58' W
Venado Beach, 8°55' N, 79°36' W

Family Sigalionidae

Sthenelais maculata Hartman, 1939

Figure 1f-g

Sthenelais maculata Hartman, 1939, pp. 64-65, pl. 15, figs. 176-187.

Material examined: Boca Grande, 8 April 1971 (2); Naos Island, 30 June 1969 (2), 29 August 1969 (1); Jaco, 21 March 1971 (1); Playa Cocal, 28 February 1971 (2).

Distribution: *Sthenelais maculata* was originally described on material from Peru, Panama, and Mexico. The present records cover Pacific beaches in Costa Rica and Panama and one beach on the Atlantic side of Colombia.

Remarks: The present specimens fit very well with the specimens originally described by Hartman (1939). The superior part of the presetal lobe is deeply bifid (Fig. 1f); the distal tooth of the composite falcigers (Fig. 1g) is strongly curved.

Family Pisionidae

Pisone remota (Southern, 1914)

Figure 2a

Praegeria remota Southern, 1914, pp. 61-64, pls. VII and VIII, figs. 15a-k.

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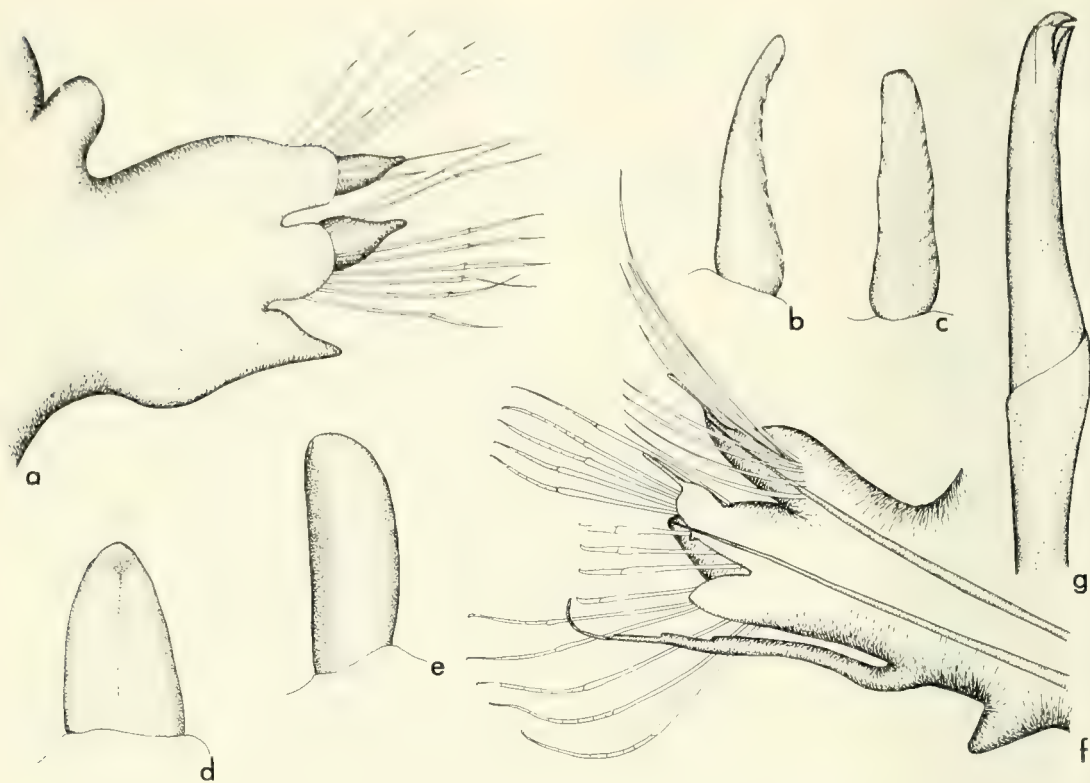


Figure 1. *Glycera abbranchiata* Treadwell: a, median parapodium, posterior view, $\times 95$; b, tall proboscideal organ, lateral view, $\times 385$; c, tall proboscideal organ, frontal view, $\times 385$; d, short proboscideal organ, frontal view, $\times 385$; e, short proboscideal organ, lateral view, $\times 385$; *Sthenelais maculata* Hartman: f, parapodium 85, anterior view, $\times 95$; g, composite falciger, parapodium 85, $\times 950$.

Pisone remota Hartman, 1968, pp. 181–182, 5 figs.

Material examined: Playa Espadilla, 1 March 1971 (1); Playita Blanca, 9 February 1971 (8).

Distribution: *Pisone remota* has been reported from shelf-areas off Ireland and on the west coast of the Americas; the present records are from the Pacific side of Costa Rica.

Remarks: The present specimens agree with *P. remota* as characterized by Hartman (1968) and with Laubier's (1967) review of the species of *Pisone*. The simple bifid hooks have a series of long, neatly organized hairs between the two teeth (Fig. 2a). This brush-border is usually illustrated as being considerably less extensive than it is in the present specimens. Paired bosses are present lateral to the base of the secondary tooth in all simple hooks.

Pisionidens indica (Aiyar and Alikuhni, 1940)

Pisionella indica Aiyar and Alikuhni, 1940, pp. 89–107, pls. 1–2, 9 text figs.

Pisionidens indica Aiyar and Alikuhni, 1943, p. 120; Siewing, 1954, pp. 81–83, pl. 23; Day, 1967, p. 133, fig. 4.I.f–j.

Material examined: Cahuita South, 1 April 1971 (2); Pradomar Beach, 21 April 1971 (1); Rodadero Beach, 26 April 1971 (22).

Distribution: *Pisionidens indica* is known from India, South Africa (Day, 1967) and has been reported from El Salvador and Brazil (Siewing, 1954). The present records are from the Atlantic side of Colombia and Costa Rica.

Remarks: The present specimens fit very well with the species as originally described and later revised by Siewing (1954).

Family Amphinomidae

Hermodice carunculata (Pallas, 1766)

Hermodice carunculata Fauvel, 1914, pp. 113–116, pl. 8, figs. 22–27, figs. 31–32; Monro, 1933a, p. 4; Hartman, 1951, pp. 22–25, fig. 1.

Material examined: Pina Beach, 24 July 1969 (1); San Blas, 19 August 1969 (1).

Distribution: *Hermodice carunculata* was originally described from the West Indies; it has been reported extensively from warm water areas in the Atlantic Ocean and is apparently limited to this ocean.

Remarks: *Hermodice carunculata* resembles *Eurythoe complanata* with which it is often confused by non-specialists, in that both species are long-bodied fire-worms. The two species differ most noticeably in the development of the caruncle. This structure is long and flexuose with poorly developed, usually completely hidden, lateral folds in *E. complanata*; it is wide and ovate, with very obvious lateral folds in *H. carunculata*.

Family Phyllodocidae

Anaitides near *multiseriata* Rioja, 1941

Anaitides multiseriata Rioja, 1941, pp. 684–687, pl. 1, figs. 2–6; Hartman, 1968, pp. 237–238, 4 figs.

Material examined: Playa Juan Chaco, 5 September 1971 (1); Venado Beach, 14 July 1969 (17).

Distribution: *Anaitides multiseriata* is known from western Mexico and Southern California; the present records are from Pacific Panama and Colombia.

Remarks: The present specimens agree with *A. multiseriata* in most characters, but differ in the color pattern. *Anaitides multiseriata* has a series of dark transverse bars with light-colored mid-dorsal spots; the specimens reported herein are nearly uniformly grey. In addition, *A. multiseriata* has a characteristic H-shaped pattern on the prostomium; this pattern is absent in the present specimens. The dorsal cirri are slightly more pointed in the present specimens than in *A. multiseriata*. Further identification will have to await a complete re-evaluation of the specific characters used to separate the many species in the genus *Anaitides*.

Family Nereidae

Ceratonereis mirabilis Kinberg, 1866

Ceratonereis mirabilis Kinberg, 1866, p. 170.

Ceratonereis tentaculata Kinberg, 1866, p. 170; Monro, 1933a, p. 45; Hartman, 1940, p. 218, pl. 35, fig. 47.

Material examined: Naos Island, 30 June 1969 (1); Rodadero Beach, 20 April 1971 (1).

Distribution: *Ceratonereis mirabilis* is widespread in warm waters and may be circumtropical; it has been reported more frequently from rocky shores than from sandy beaches.

Remarks: *Ceratonereis mirabilis* has a distally bifid prostomium and very long antennae. The

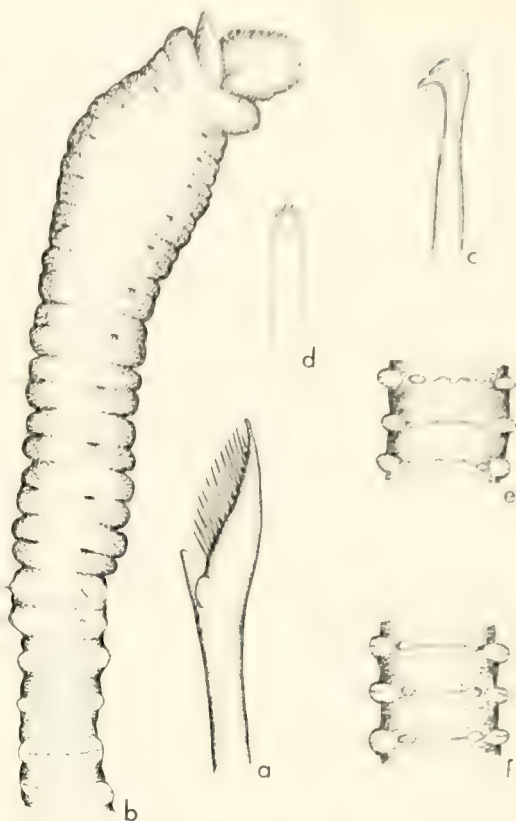


Figure 2. *Pisione remota* (Southern): a, simple hook, $\times 1900$; *Notodasus dexterdae*, new species: b, anterior end, lateral view, $\times 16$; c, hooded hook, lateral view, $\times 950$; d, hooded hook, frontal view, approx. $\times 950$; e, abdominal setigers 8–10, dorsal view, $\times 16$; f, abdominal setigers 15–17, dorsal view, $\times 16$.

dorsal cirri are greatly prolonged in posterior setigers giving the specimens a slightly ragged appearance.

Nereidae, indeterminable

Material examined: Rodadero Beach, 20 April 1971 (fragment).

Remarks: This fragment cannot be further identified; it appears different from *Ceratonereis mirabilis* reported from the same beach.

Family Glyceridae

Glycera abbranchiata Treadwell, 1901

Figure 1a–e

Glycera abbranchiata Treadwell, 1901, pp. 200–201, fig. 49; Jones, 1962, p. 183, figs. 41–48.

Material examined: Naos Island, 31 July 1969 (8).

Distribution: *Glycera abbranchiata* is known from Puerto Rico, Jamaica, and the Lesser Antilles. The present record is from Pacific Panama and is the first record of the species outside the western Atlantic Ocean.

Remarks: The present specimens resemble *G. tessellata* Grube (1863) in general body proportions and in the shape of the parapodia. The two postsetal lobes (Fig. 1a) are somewhat more distinct in *G. abbranchiata* than in *G. tessellata* and the two presetal lobes are somewhat longer in the former than in the latter.

The proboscideal organs are of two different kinds. The most numerous kind (Fig. 1b-c) is narrow and slender and has 13 to 14 ribs in an oblique pattern. The other kind (Fig. 1d-e) is considerably wider and show a broad flattened shape; this second kind lacks ribs.

The distinctness of *G. abbranchiata* was recognized by Jones (1962) who re-examined the type material. These types were also examined during the present investigation and were found to be as described by Jones.

Hemipodus armatus Hartman, 1950

Hemipodus armatus Hartman, 1950, pp. 83-84, pl. 12, figs. 1-5.

Material examined: Boca Grande, 28 April 1971 (3); Cahuita South, 1 April 1971 (1); Puerto Viejo, 2 April 1971 (1); Samara, 8 April 1971 (9); Tamarindo, 9 April 1971 (1 large, several small).

Distribution: *Hemipodus armatus* is known from western Mexico in shallow-water; the present records come from sandy beaches on both Atlantic and Pacific sides of the isthmus of Panama.

Remarks: The present specimens agree with *H. armatus* in that the tall proboscideal organs have numerous transverse ridges and in that the presetal lobes of median and posterior parapodia have slender digitate distal processes.

Family Nephtyidae

Nephtys singularis Hartman, 1950

Nephtys singularis Hartman, 1950, pp. 98-100, pl. 15, figs. 1-6.

Material examined: Naos Island, 30 June 1969 (6); Jaco, 27 March 1971 (3); La Punta, 14 March 1971 (8); Samara, 8 April 1971 (2); Tamarindo, 9 April 1971 (28).

Distribution: *Nephtys singularis* was described from Guatemala and western Mexico; all present records are from the eastern Pacific Ocean in somewhat lower latitudes.

Remarks: The present specimens agree with

the original description. Interramal cirri are present from setiger 4 in nearly all specimens, but can be identified from setiger 3 in very large specimens. The superior neuropodial lobes are best developed in setigers 8-15 and are completely reduced posterior to setiger 30 in all specimens.

Family Onuphidae

Americonuphis, new genus

Type species: is *A. magna* (Andrews, 1891, as *Diopatra*); *A. hartmanae* (Friedrich, 1956) and *A. reesei*, new species also belong to this genus.

Description: *Americonuphis* includes macropodous onuphids with the anterior five or more parapodia enlarged and armed with composite falcigers. More posterior parapodia have simple limbate and pectinate setae, and distally bifid subacicular hooks. The prostomium has five occipital tentacles, each has a multiannulate base and a long, tapering style. The peristomium has a pair of tapering cirri. The thick, long, enlarged parapodia are armed with composite falcigers; the setal shafts are limited to their respective segments. The long, cirriform dorsal and ventral cirri taper distally. Farther back the ventral cirri are replaced by thick, glandular pads. Branchiae are present behind the modified segments and are continued through many segments; each has many filaments in a pectinate arrangement. The maxillary apparatus resembles that of other onuphids.

Remarks: *Americonuphis* is most nearly allied to *Rhamphobrachium* in having five or more, instead of two or three, anterior parapodia greatly enlarged and armed with special setae. The two genera differ in that the former have composite falcigers instead of scythe-like curved spines in these setigers and in that the shafts of the setae are limited to one segment rather than continued through several segments.

Americonuphis reesei, new species

Figure 3a-e

Material examined: Gulf of Panama, 27 m, mud, coll. E. Reese (1, Holotype); Naos Island, 3 July 1969 (1).

Description: The large holotype has been removed from a thick, mud-walled tube and is broken into several pieces; the posterior end is absent. The anterior fragment, with 80 setigers, measures 85 mm long and 8 mm wide; more posterior segments bring the total length to 230 mm and the width to 9 mm; the total number of segments exceeds 300. The anterior ventrum and the parapodial bases are mottled with black pigment. The tube has an inner lining of a tough parchment-like material and is externally covered with a thick layer of mud.

The small prostomium is a flat rectangular lobe, slightly longer than wide on top of the thick, biarticulate palps. A pair of tapering frontal antennae are present. The thick ventral palps are basally fused and are deeply divided distally; their bases are large and overlie the oral aperture (Fig. 3a). The ventral lip is formed by the thick, broad anterior edge of the peristomium. A pair of eyes is at the outer bases of the inner lateral occipital tentacles.

The five occipital tentacles are arranged so that three are in a row across the posterior end of the prostomium; the other two are in front of the inner lateral pair and at the sides of the prostomium. The ceratophores are annulated; each of the median and inner lateral ones has six short and a much longer distal article; the outer lateral ceratophores have only five short articles in addition to the distal long one. The long ceratostyles are tapering; the median is the longest and reach setiger 11. The peristomium is longer than the succeeding segments; its cirri are long, smooth and tapering; each is nearly twice as long as the peristomium.

The first five pairs of parapodia (Fig. 3a) are enlarged; the first are at the sides of the prostomium, and the others are increasingly ventral so that the two of a pair nearly meet medially and are separated by a quadrate mid-ventral pad. Parapodia are sub-biramous; the notopodia are represented by a fascicle of slender acicula projecting into the long, tapering dorsal cirri; the ventral cirri are similar, but only about half as long (Fig. 3b). The base of the first parapodium is transversely wrinkled as though capable of great lateral extension. Pre- and postacicular lobes are distally prolonged to extend beyond the setal tips. Setae number twelve to fourteen in a fascicle; each is a composite falciger (Fig. 3c) terminating on a bifid tip and a short hood. These falcigers are accompanied by three to five simple, capillary setae resembling the imbedded notacicula.

The second, third, and fourth parapodia are more modified and directed forward on the ventrum; their setae resemble those in the first setiger. The ventral cirri are cirriform in these setigers; thereafter they are replaced by thick pads.

Branchiae are first present from setiger 6 with three filaments in a pectinate arrangement. The maximal number of branchial filaments is seven and is found on the twelfth branchial setiger (Fig. 3d). The dorsal cirri in these setigers are short and tapering.

Parapodia behind the modified setigers have long, limbate setae and one or two yellow subacicular hooks, first present from setiger 15; they are distally bifid. Pectinate setae are numerous; each is distally flared and terminated in many short dentitions (Fig. 3e). Acicula number two or three in a ramus; each is yellow, nearly straight and terminates in a slightly acute tip.

The maxillary apparatus (seen in dissection) is well developed. Maxilla I is the forceps; maxilla II

has ten teeth left and twelve right; III has fourteen left and nine right; IV has four left and is absent on the right-hand side; V has one tooth on each side.

Distribution: *Americonuphis reesei* is known from two localities in the Gulf of Panama, one in muddy bottoms in 27 m, the other intertidally in a sandy bottom.

Remarks: *Americonuphis reesei* differs from *A. hartmanae* (Friedrich, 1956) in that it has five anterior modified setigers rather than six. The composite falcigers are bifid in the former and entire in the latter. In addition, *A. reesei* differs from *A. magna* in the number of teeth on the different jaw-pieces and *reesei* has about six, rather than twelve branchial filaments where the branchiae are best developed.

Americonuphis hartmanae (Friedrich, 1956),
new combination

Rhamphobranchium hartmanae Friedrich, 1956, pp. 63–65, fig. 5a–c.

Distribution: Playa de las Flores, El Salvador in an intertidal sandy beach.

Remarks: The specimens described by Friedrich (1956) appear to have been as large as those described for *A. reesei*. The first six parapodia are enlarged and ventrally directed; parapodia 7 and 8 are transitional; the remainder of the parapodia are not modified and are lateral in position. Eyes are absent and the median occipital tentacle reaches back to setiger 5; its ceratophore has eight rings; each of the inner lateral occipital tentacles has twelve or thirteen basal rings. The modified anterior parapodia have equally long dorsal and ventral cirri and postsetal lobes. These parapodia are armed with weak simple superior setae and about four dark brown, thick, distally curved composite hooks. From setiger 7 the postsetal lobe is short. Branchiae are first present from this setiger as a single filament; the maximum number of branchial filaments is five–seven at setiger 12. Dorsal cirri are shorter than the branchial filaments; each has a curved fleshy spur at the base. Anterior ventral cirri are long through seven setigers and are absent posterior to setiger 18. Postmodified setigers have numerous limbate setae and a pair of light brown subacicular hooks. Pectinate setae are present from setiger 11 and number three or four in a fascicle.

Diopatra obliqua Hartman, 1944

Diopatra obliqua Hartman, 1944a, pp. 57–61, pl. 2, figs. 24–36, pl. 16, figs. 331–333; Fauchald, 1968, pp. 9–10, pl. 2, fig. a.

Material examined: Naos Island, 29 August 1969 (1).

Distribution: *Diopatra obliqua* is common along the coast from Golfo de California, Mexico to Peru in the eastern Pacific Ocean.

Remarks: *Diopatra obliqua* has bidentate hooded hooks in anterior setigers and strongly oblique pectinate setae. Details of the first parapodia were described by Fauchald (1968).

Diopatra splendidissima Kinberg, 1856

Diopatra splendidissima Hartman, 1944a, pp. 56–57, pl. 1, figs. 21–23; Fauchald, 1968, pp. 12–13, pl. 2, fig. j.

Material examined: Venado Beach, 14 July 1969 (1).

Distribution: *Diopatra splendidissima* is known from southern California to Ecuador in the eastern Pacific Ocean.

Remarks: *Diopatra splendidissima* has bidentate hooded hooks in the anterior setigers; the pectinate setae are transverse; each has a few coarse teeth. A description of the first parapodia was added by Fauchald (1968).

Family Lumbrineridae

Lumbrineris monroi Fauchald, 1970

Lumbrineris monroi Fauchald, 1970, pp. 99–102, pl. 16, figs. e–i.

Material examined: Naos Island, 30 July 1969 (1).

Distribution: *Lumbrineris monroi* is known from western Mexico in shallow water; the present record is from a sandy beach in Pacific Panama.

Remarks: The present specimen differs from the species as originally described in that the simple hooded hooks are present from setiger 12 rather than from setigers 18–24 and in that the posterior postsetal lobes are slightly prolonged. The specimen is similar in size to the holotype.

Lumbrineris zonata (Johnson, 1901)

Lumbriconereis zonata Johnson, 1901, pp. 408–409, pl. 9, figs. 93–100.

Lumbrineris zonata Hartman, 1944a, pp. 146–147; Fauchald, 1970, pp. 112–113, pl. 18, figs. e–i.

Material examined: Venado Beach, 14 July 1969 (1).

Distribution: *Lumbrineris zonata* was described from Washington on the west coast of North America and has previously been reported as far south as Baja California. The present record is from the Pacific coast of Panama.

Remarks: *Lumbrineris zonata* has hooded hooks present from the first setigers and the postsetal lobes are short in all setigers. The present

specimens do not appear to differ from specimens found in southern California or off western Mexico.

Family Orbiniidae

Orbinia johnsoni (Moore, 1909)

Aricia johnsoni Moore, 1909, pp. 260–262, pl. 8, figs. 30–33.

Orbinia johnsoni Hartman, 1969, pp. 33–34, 4 figs. *Material examined:* Samara, 8 April 1971 (13).

Distribution: *Orbinia johnsoni* is previously known from central and southern California and from Costa Rica, where the present record is from.

Remarks: *Orbinia johnsoni* has the transition between thorax and abdomen between setigers 16–19 according to Hartman (1969). The present specimens all have this transition at setiger 18. Branchiae are present from setiger 15 in all specimens. The ventral row of papillae on the transitional setigers is rather poorly developed.

Family Paraonidae

Paraonides platybranchia (Hartman, 1961)

Paraonis platybranchia Hartman, 1961, pp. 86–87.

Paraonides platybranchia Hartman, 1969, pp. 73–74, 2 figs.

Material examined: Naos Island, 30 June 1969 (154).

Distribution: *Paraonides platybranchia* was originally described from southern California; the present record is the first from other areas and may indicate a wider distribution in the Pacific Ocean.

Remarks: The present specimens agree with *P. platybranchia* in that they have branchiae present from setiger 4 through setigers 29–30. They lack antennae and modified setae.

Family Spionidae

Dispio uncinata Hartman, 1951

Dispio uncinata Hartman, 1951, pp. 87–90, pl. 22, figs. 1–5, pl. 23, figs. 1–4; Hartman, 1969, pp. 105–106, 3 figs; Foster, 1971, pp. 73–78, figs. 161–174.

Material examined: Naos Island, 30 June 1969 (4); Shimmey Beach, 15 August 1969 (1).

Distribution: *Dispio uncinata* is known from both coasts of North and Central America in shallow water and intertidal areas in sand.

Remarks: Foster (1971, pp. 76–78) discussed the possible relationship between the present species, *D. schusteri* and *D. remanei* Friedrich (1956) from El Salvador. The three species are very similar, but synonymizing the three species must await a re-examination of the type materials of all three.

Paraprionospio species indeterminable

Material examined: Naos Island, 30 June 1969 (1).

Remarks: The present specimen cannot be identified to species. It is small and rather badly preserved; two pairs of pennate brachiae are present starting on the third setiger; scars from branchiae on other segments could not be identified.

Foster (1971, pp. 79–112) revised the species usually assigned to *Prionospio* distributing them on several genera. The characters used were the number and structure of the branchiae. This makes generic identification of poorly preserved material difficult on occasion, but is probably the best alternative available.

Foster (1971, p. 112) also synonymized all species assigned to the genus *Paraprionospio* into a single species, *P. pinnata* (Ehlers, 1901, pp. 163–164). It is not clear from Foster's article that she had material of all the different species involved. Synonymies based solely on descriptions are not acceptable to the present author; experience has shown that differences often exist between populations of closely related species, and that these differences often have escaped description. It is thus necessary to compare materials directly, preferably of course type materials, but if such are not available, at least materials from the type locality or the immediate vicinity.

Scolelepis agilis (Verrill, 1873)

Nerinides agilis Hartman, 1956, p. 291.

Material examined: Airport Beach, 19 March 1971 (28); Boca Barrancas, 13 March 1971 (73); Boca Grande 28 April 1971 (11); Cahuita South, 1 April 1971 (2); Naos Island, 30 June 1969 (52); La Punta, 14 March 1971 (418); Playa Juan Chaco, 9 May 1971 (22); Pradomar Beach, 21 April 1971 (1); Puerto Viejo, 2 April 1971 (4); San Blas, 18 August 1969 (4); Shimmey Beach, 10 August 1969 (101).

Distribution: *Scolelepis agilis* is known from the western Atlantic coasts from New England to Central America; the present records are also from the Pacific side of Central America.

Remarks: Foster (1971, pp. 59–63, figs. 118–131) following Pettibone (1963, p. 92) synonymized this species with the European *S. squamata* (Müller, 1806, for complete reference see Pettibone, 1963). It is unclear from Foster and Pettibone whether they examined any material from European waters or used the current descriptions as the base for this synonymy. Until this point has been cleared up, it seems preferable to keep materials from the Americas separate from the

European materials, even if the descriptions overlap.

Spionidae, species indeterminable

Material examined: Playita Blanca, 9 February 1971 (4).

Remarks: The present specimens are very badly preserved and can be recognized as spionids only on the distribution of the setae. The hooded hooks are bifid.

Family Magelonidae

Magelona riojai Jones, 1963

Magelona riojai Jones, 1963, pp. 9–14, figs. 22–35.

Material examined: Jaco, 27 March 1971 (3).

Distribution: *Magelona riojai* was originally described from Veracruz, Mexico, and Florida, USA. The present record is from Jaco, Costa Rica on the Pacific side of Central America.

Remarks: The present specimens fit very well with *M. riojai*; the anterior end is somewhat more truncate than as illustrated by Jones (1963, fig. 22) and the mucronate tips of the modified setae of setiger 9 are slightly slenderer than the ones illustrated by Jones.

Family Cirratulidae

Cauleriella alata (Southern, 1914)

Chaetozone alata Southern, 1914, pp. 112–113, pl. 12, figs. 27a–d.

Cauleriella alata Hartman, 1969, pp. 225–226, 3 figs.

Material examined: Naos Island, 30 July 1969 (8), 29 August 1969 (17).

Distribution: *Cauleriella alata* has been reported from sandy beaches from worldwide areas. The relationship between the different populations is unknown and it is doubtful that they can be adequately characterized on morphological characters alone.

Remarks: The present specimens agree with *C. alata* in that they have bifid hooks present from the first neuropodium and have a pair of deeply imbedded black eyes. The bifid condition of the hooks is less obvious than as originally described, but is distinct in all setigers.

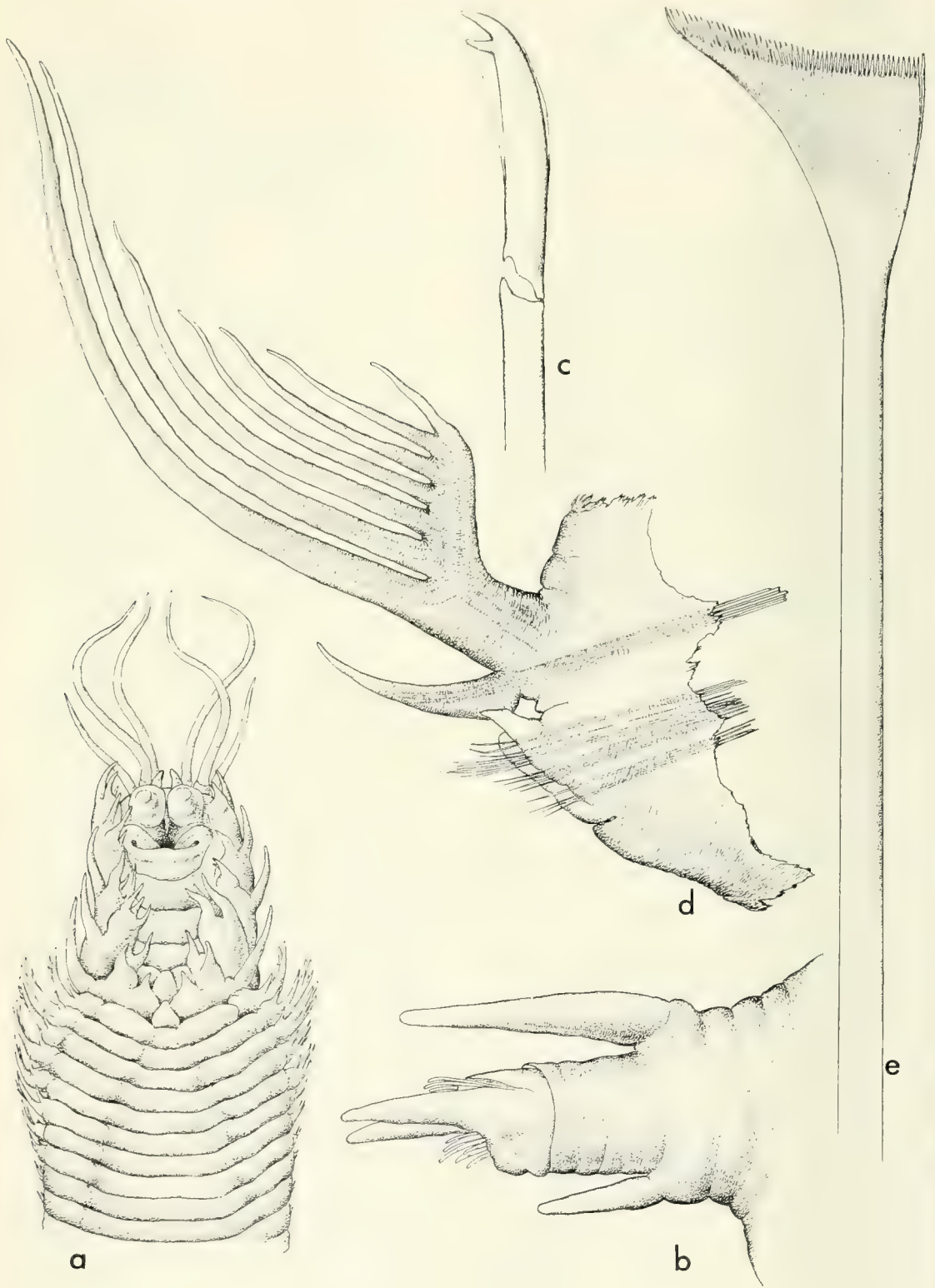
Cirratulus ? cirratus (Müller, 1776)

Cirratulus cirratus Hartman, 1969, pp. 245–246, 2 figs.

Material examined: Naos Island, 30 June 1969 (2), 29 August 1969 (2).

Distribution: *Cirratulus cirratus* is cosmopolitan in relatively shallow water; mostly in soft bottoms.

Remarks: The present specimens belong to the genus *Cirratulus* in that they have transverse rows



of tentacles on the first setiger and acicular spines present from an anterior setiger. Neuropodial spines are first present from setiger 12–14 rather than from setigers 6–11 as in *C. cirratus*. This character is considered important in identifying the different species of *Cirratulus*, so the present specimens are tentatively assigned to *C. cirratus*.

Family Flabelligeridae

Piromis americana (Monro, 1928)

Stylarioides capensis americana Monro, 1928, pp. 96–97, fig. 16; Monro, 1933b, pp. 1057–1058, text fig. 6.

Piromis americana Hartman, 1969, pp. 305–306, 3 figs.

Material examined: San Carlos, 4 August 1969, in tubes under rock at low tide (1).

Distribution: *Piromis americana* is known from Panama to central California.

Remarks: The present specimen agrees with those described by Monro, except that the neurosetae are somewhat less distinctly striated.

Family Opheliidae

Armandia ? *bioculata* Hartman, 1938

Armandia bioculata Hartman, 1938, pp. 105–106, figs. 51–54; Hartman, 1969, pp. 323–324, 3 figs.

Material examined: Naos Island, 30 July 1969 (2).

Distribution: *Armandia bioculata* is known from Washington to California in sandy intertidal areas. The present records come from Panama in a similar environment.

Remarks: Both specimens are incomplete posteriorly; they resemble in all identifiable characters specimens of *A. bioculata* from California.

Euzonus (*Thoracophelia*) *furciferus* (Ehlers, 1897)

Thoracophelia furcifera Ehlers, 1897, pp. 101–103, pl. 7, figs. 164–167.

Euzonus (*Thoracophelia*) *furciferus* Hartman, 1959, p. 431.

Material examined: Playa Espadilla, 1 March 1971 (2).

Distribution: *Euzonus furciferus* was originally described from intertidal areas in Punta Arenas, Chile; the present record comes from a similar environment in Pacific Costa Rica.

Remarks: The present two specimens fit with the species as originally described, including the numbers of setigers in the different parts of the body, the shape of the branchiae and the number and shape of the anal cirri.

Family Capitellidae

Notodasus dexteræ, new species

Figure 2b–l

Material examined: Naos Island, 30 July 1969 (30 TYPE).

Description: The holotype is an incomplete specimen with 29 setigers that is 17 mm long and 1 mm wide. The anterior end is inflated; the rest of the body is cylindrical. The specimens are greyish yellow in color. The peristomium and the first five setigers are strongly areolated (Fig. 2b); the remainder of the thoracic setigers less so. All thoracic segments are biannulated; the abdominal segments are single-ringed.

The prostomium is a flattened conical structure; the peristomium is considerably wider and is anteriorly inflated. All eleven thoracic setigers are biramous and the setal bundles emerge from deep pockets.

The two first abdominal setigers have short, conical parapodia; both noto- and neuropodia are similar and setae emerge from conical protuberances rather than from pockets as in the thorax. All later abdominal setigers (Fig. 2e) are similar; the neuropodia are long welts that are separated ventrally only by the ventral nerve cord. The neuropodia are long enough laterally to be visible from the dorsal side. The large, nephridial papillae above the neuropodia are on the dorsal side, and medial to these papillae near the dorsal midline, are two slightly raised ridges which represent the notopodia. These ridges have setae only in the abdominal parapodia 3 to 14; further posteriorly, the notopodia are completely reduced. In these posterior setigers, (Fig. 2f), the nephridial papillae are connected across the dorsum by a ciliated ridge.

All thoracic setigers and the first two abdominal setigers have pointed, capillary setae only. The remaining abdominal setigers have hooded uncini only. Each uncinus (Figs. 2c–d) has a large main fang and a crest of nine smaller teeth. These teeth are arranged so that there are five in a lower row, three in the next row and a single tooth above the others. The margin of the hood is smooth.

Figure 3. *Americonuphis reesei*, new genus, new species: a, anterior end, ventral view, $\times 7$; b, first parapodium, anterior view, $\times 45$; c, distal end of composite falciger from first parapodium, lateral view, $\times 540$; d, branchial parapodium, anterior view, $\times 46$; e, pectinate seta, full view, $\times 1090$.

TABLE 1. Geographical distribution of polychaetes reported from Central American sandy beaches.

Species	Previously known distribution
I. SPECIES FOUND IN ATLANTIC BEACHES	
<i>Pisionidens indica</i>	Circumtropical
<i>Hermodice carunculata</i>	Western Atlantic, warm waters
II. SPECIES FOUND IN PACIFIC BEACHES	
<i>Pisone remota</i>	Cosmopolitan
<i>Anaitides near multiseriata</i>	Eastern Pacific, warm waters
<i>Glycera abbranchiata</i>	Western Atlantic, warm waters
<i>Nephtys singularis</i>	Eastern Pacific, warm waters
<i>Americonuphis reesei</i>	Eastern Pacific, warm waters
<i>Diopatra obliqua</i>	Eastern Pacific, warm waters
<i>D. splendidissima</i>	Eastern Pacific, warm waters
<i>Lumbrineris monroi</i>	Eastern Pacific, warm waters
<i>L. zonata</i>	Washington-Baja California
<i>Orbinia johnsoni</i>	Eastern Pacific, warm waters
<i>Paraonides platybranchia</i>	Eastern Pacific, warm waters
<i>Magelona riojai</i>	Western Atlantic, warm waters
<i>Caulerella alata</i>	Cosmopolitan
<i>Cirratulus ?cirratus</i>	Cosmopolitan
<i>Piromis americana</i>	Eastern Pacific, warm waters
<i>Armandia ?bioculata</i>	Washington-Southern California
<i>Euzonus (Thoracophelia) furciferus</i>	Chile
<i>Notodasus dexteræ</i>	Eastern Pacific, warm waters
<i>Chone minuta</i>	Central and southern California
III. SPECIES FOUND ON BOTH SIDES OF THE ISTHMUS OF PANAMA	
<i>Sthenelais maculata</i>	Eastern Pacific, warm waters
<i>Ceratonereis mirabilis</i>	Circumtropical
<i>Hemipodus armatus</i>	Western Mexico
<i>Dispio uncinata</i>	The Americas, warm waters
<i>Scoelepis agilis</i>	Western Atlantic, warm waters

Distribution: *Notodasus dexteræ* is known from intertidal sands on an island off Panama.

Remarks: The genus *Notodasus* was previously represented by one species; *N. magnus* which was described from deep water off western Mexico by Fauchald (1972:246-247, pl. 51, fig. a-c). *Notodasus magnus* has notopodia developed in all abdominal setigers and the neuropodium is absent in the first thoracal setiger whereas, *N. dexteræ* lacks notopodia in posterior abdominal setigers and all thoracal setigers are complete.

It gives me pleasure to name this species after Deborah Dexter of California State University, San Diego who collected this very interesting material.

Family Sabellidae

Chone minuta Hartman, 1944

Chone minuta Hartman, 1944b, pp. 280-281, pl. 23, figs. 50-52, pl. 24, figs. 59-60; Hartman, 1969, pp. 671-672, 5 figs.

Material examined: Naos Island, 29 August 1969 (8); Playita Blanca, 9 February 1971 (1).

Distribution: *Chone minuta* is known from central and southern California in rocky areas. The present records are from Costa Rica and Panama in sandy beaches, but as indicated above, the specimens cannot be separated from *C. minuta* as presently described.

Remarks: The present specimens agree with *C. minuta* in that the spatulate setae are sharply mucronated; the radioloi are united very high up on the crown and the number of segments is similar to that described for the species from central California.

DISCUSSION

Twenty-six species were found in the present collections; nineteen were in material from the Pacific Ocean only (Table 1) and of these, fourteen have their total distribution limited to the eastern Pacific Ocean. Three species are presumed to be cosmopolitan, but have not been

found on the western Atlantic coasts of Central America. Two species previously were recorded from the Caribbean Sea only, but we did not find them in our collections from the Atlantic coasts. Two species have been found in beaches on the Atlantic coast only; one of these appears limited to warm water in the Atlantic Ocean; the other has a reported circumtropical distribution, but was absent from our eastern Pacific collections. Five species have been found in sandy beaches on both sides of the isthmus of Panama; two were previously known only from the eastern Pacific, one had been reported only from western Atlantic areas, another has been known from both coasts of the Americas, and one is circumtropical.

A total of 24 species were found in the Pacific beaches and only seven in the Atlantic beaches. This difference may appear puzzling since the eastern Pacific Ocean usually is considered impoverished when compared to other faunal areas at similar latitudes (Ekman, 1953:39-44). This is demonstrable for hard-bottom faunas, e.g. coral reefs, but a close investigation of the lesser known soft-bottom areas may very well change our views of the faunal relations between the two oceans.

Under some circumstances, the difference in numbers of species of polychaetes might be due to a sampling bias; this cannot be the case in this instance since the same investigators sampled beaches in both areas.

Dexter (1972) discussed the community structure of two Panamanian beaches, one on each side of the isthmus. Some of her material is treated above. Dexter demonstrated that the variation in the physical parameters was greater on the Pacific coast than on the Atlantic coast due to upwelling and that this upwelling had been associated with a greater primary productivity on the west coast. In terms of the organisms present, Dexter's survey shows that the whole fauna is distributed essentially as is the polychaete fraction with the numbers of species and the biomass very much higher on the Pacific than on the Atlantic coast. The species diversity is lower on the Pacific coast than on the Atlantic side. This lower species diversity is probably related to the lower stability in physical parameters on the Pacific coast. The higher numbers of species of polychaetes and the higher biomass probably are related to the higher productivity on the west coast. There is no contradiction between this result and the previous findings of a depauperized fauna on the Pacific side. The earlier conclusion was based on the coral reef fauna and the tem-

perature variation on the Pacific coast is so great (Dexter, 1972:449) that only a limited number of reef species are able to survive. Species burrowing in sand and mud are apparently not as sensitive to temperature fluctuations as their hard-bottom relatives.

ACKNOWLEDGMENTS

The author is very grateful to Deborah M. Dexter, who collected the material. Olga Hartman made the first description of *Americonuphis reesei* and allowed the author to use this as the base for the present description. The excellent drawings of this species were made by Anker Petersen.

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POLYCHAETOUS ANNELIDS COLLECTED BY THE R V *HERO* FROM BAFFIN ISLAND, DAVIS STRAIT, AND WEST GREENLAND IN 1968

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ABSTRACT: Seventy-one species of polychaetes are reported from four benthic stations in the eastern Canadian Arctic. Two new species were found and described by Blake, 1972. *Myriochele oculata* was found to be abundant off Baffin Island and is redescribed and compared with *M. heeri*; one new synonym is presented. Aspects of the faunal analysis are discussed and compared with other Arctic areas.

Benthic ecology has been studied in east Greenland fjords (Thorson, 1933, 1934, 1944; Sparck, 1933; Madsen, 1936; Bertelsen, 1937; Degerbøl, 1937; and Ockelman, 1958), from scattered points along the west coast of Greenland (Vibe, 1939, 1950; Madsen, 1940; and Petersen, 1962) and the Baffin Island-Labrador coast (Packard, 1867, 1891; Soper, 1928; Ellis and Wilce, 1961; see Ellis, 1960 for further references). All of this benthic ecological work has been conducted in inshore areas (fjords, sounds, inlets, etc.); practically nothing is known about the biology of the fauna inhabiting the continental shelves. Of particular interest is the polychaete component. Our

knowledge of the polychaete fauna of this general area has been supplemented by several workers, especially Packard (1863, 1867), Moore (1902, 1909), Thorson (1936), Treadwell (1937), Berkeley and Berkeley (1943), Wesenberg-Lund (1934, 1947, 1948, 1950a, 1950b, 1951, 1953), Vibe (1950), Grainger (1954), Pettibone (1956) and Curtis (1970). Thorson (1934) found that infaunal biomass generally decreased with increas-

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ing depth, that lamellibranchs dominate the fauna of shallow water, and that polychaetes dominate in deeper water. Ellis (1960) substantiates Thorson's findings. The polychaete fauna of the deeper waters of the Davis Strait and the Labrador Sea is inadequately known.

At least 134 species of polychaetes have been reported from the eastern Canadian Arctic and subarctic waters (Grainger, 1954) and from west Greenland (Wesenberg-Lund, 1950a).

During August of 1968, the University of Maine participated in the shakedown cruise of the National Science Foundation's new polar research vessel, the R V HERO, to the eastern Canadian Arctic.

Invertebrate studies were conducted by the University of Maine in the Labrador Sea and Davis Strait. Although the primary mission of the cruise was to test the vessel in Arctic waters, it was possible to sample 32 biological stations in Arctic and subarctic waters. Four of these stations were benthic and the remainder planktonic. Two brief accounts of the cruise and progress in analysis of the data have been published (Dearborn and Dean, 1969; 1970). Another benthic station (Number 33), sampled near the end of the cruise in the Gulf of Maine, is not included.

The present paper reports on the benthic polychaetous annelids collected during the cruise. In subsequent papers other personnel will report on the echinoderms, molluscs, zooplankton, and phytoplankton.

Station data and polychaete species obtained at the benthic stations are given below. The four benthic stations include use of both standard and specialized gear. Standard gear included a Ponar type grab (0.1 m²), Peterson grab (0.1 m²), Rock dredge, Triangular dredge, Tri-net trawl, Mop tangle, and underwater camera. Specialized gear included a modified Beyer Epibenthic sled (Holme, 1964) equipped with a Clarke-Bumpus closing device and a "mouse-trap" sampler (Muus, 1964). The Epibenthic sled was towed along the bottom to obtain a plankton sample from about 0.5 m above the bottom, while the "mouse-trap" was used to collect a 225 cm² sample of the top 1–2 cm of bottom substrate.

Polychaetes were screened on board ship and preserved as soon as possible after collection. Propylene phenoxylol (0.15%) was used as a narcotizing agent and either formalin or Bouin's fluid was used as a fixative. After fixation the material was preserved in 70% ethyl alcohol. Identifi-

cation and sorting were done at the Ira C. Darling Center during 1968–1969.

The collections remain at the Ira C. Darling Center, pending completion of the remaining invertebrate studies. At that time, the entire collection will be transferred to the United States National Museum, Washington, D.C.

RESULTS

Seventy-one species of Polychaeta are distributed in 27 families; two species are new to science. Details of these species have been presented in another paper (Blake, 1972). The Polynoidae and Sabellidae are best represented in the collections with seven and eight species, respectively.

The names and numbers of polychaetes taken at the four benthic stations are presented below. A systematic list summarizes the species collected.

LIST OF BENTHIC STATIONS

BENTHIC POLYCHAETA

HERO CRUISE No. 3

AUGUST 1968

STATION 20 East Angiak Island (Baffin Island Region); lat. 65°43' N—long. 62°05' W; 14 August 1968, 1230–1700 hours EDT (Zone 4); sediment analysis: a well-sorted ($So = \sqrt{1.9}$) brown-grey sticky mud with a mean particle size of 150 μ . Gear: Ponar grab (A and B); Mop tangle and Triangle dredge towed in tandem (E). Depth, ranged from 132–245 m.

POLYCHAETA: *Antinoella sarsi* E(1); *Pholoe minuta* A(7); *Nephtys incisa* A(1), B(1); *Sphaerodorum gracilis* A(1); *Scoloplos armiger* A(2), B(3); *Paraonis gracilis* A(1); *Prionospio steenstrupi* A(3); *Chaetozone setosa* A(30), B(46), E(1); *Cirratulus cirratus* B(1); *Scalibregma inflatum* A(2), B(1); *maldanids* A(2); *Myriochele oculata* A(36), B(47); *Myriochele heeri* A(25), B(12); *Melinna elisabethae* A(4), B(12); *Lysippe labiata* A(1); *Glyphanostomum pallescens* E(1); ampharetids A(2); *Polycirrus medusa* E(1); *Euchone papillosa* A(5), B(1), E(1).

STATION 26 Southern Baffin Bay; lat. 67°49' N—long. 60°46' W to lat. 67°38' N—long. 60°38' W; 16 August 1968, 2330–1200 hours EDT (Zone 4); bottom temperature 0.1°C; sediment, thick sticky mud. Gear: Ponar grab (A), Peterson grab (B), Niskin cast (D), Triangular dredge (E), mouse trap sampler (F), Epibenthic sled and Triangular dredge in tandem (G). The Ponar and Peterson grabs (A and B) failed to operate, but mud was retained on the corners and edges of the grabs. This mud was sieved for polychaetes as was mud retained on the weights and shackles of the Niskin cast. Depth, ranged from 1920–1745 m.

POLYCHAETA: *Eteone flava* A(1), B(1); *Pelagobia longicirrata* A(1 was caught on screen of grab as it was drawn through the water column); *Aglaophamus malmgreni* G(1); *Scoloplos* sp. A(1); *Haploscoloplos* sp. B(1); *Aricidea succica* F(5); *Phyllochaetopterus* sp. E(1); *Chaetozone setosa* A(6), B(1); *Brada villosa* G(1); *Cryptosclerocheilus baf-finensis* D(2), E(1), G(1); maldanids A(1), E(5), G(2); *Myriochele heeri* A(1); *Ampharete arctica* G(1); *Jasmincira schaudinni* E(2), G(6).

STATION 28 Davis Strait: lat. 66°28' N—long. 57°26' W to lat. 66°29' N—long. 56°42' W; 17 August 1968, 0300–0900 hours EDT (Zone 4); bottom temperature 2.58°C; sediment, soft mud composed partly of large agglutinated foraminifera. Gear: Tri-net trawl (D). Depth, ranged from 580–610 m.

POLYCHAETA: *Lactmonice filicornis* D(4); *Eunoe oerstedii* D(2); *Lagisca extenuata* D(8); *Austrolaenilla mollis* D(1); *Neoleanira tetragona* D(1); *Sphaerodorum gracilis* D(3); *Glycera capitata* D(1); *Lumbrineris latreilli* D(3); *Lumbrineris fragilis* D(1); *Lumbrineris fauchaldi* D(7); *Nothria conchylega* D(many); *Maldanella davisii* D(2); *Ampharete arctica* D(7); *Glyphanostomum pallescens* D(2); *Eupolymnia* sp. D(1); *Pista cristata* D(3); *Terebellides stroemii* D(2).

STATION 29 Off Little Hellefiske Bank (West Greenland); lat. 64°57' N—long. 58°38' W; 18 August 1968, 0800–1115 hours EDT (Zone 4); bottom temperature 1.4°C; rocky bottom with encrusting epifauna of hydroids and bryozoans. Gear: Niskin cast (A); Tri-net trawl (C); Triangular dredge (F and G). Depth, ranged from 79–85 m.

POLYCHAETA: *Eunoe oerstedii* A(2 retained on Niskin weights), *Lagisca extenuata* C(1), F(3); *Harmothoe imbricata* G(1), F(4); *Gattyana cirrosa* F(11), G(4); *Euphrosine borealis* C(4), F(6), G(2); *Eulalia bilineata* C(4), G(1); *Eumida* spp. F(1), G(1); *Typosyllis fasciata* C(10), G(6), F(3); *Typosyllis armillaris* C(4); *Exogone verugera* C(7); *Sphaerosyllis* sp. C(4); syllid C(1); *Nereis pelagica* C(9), F(6), G(1); *Glycera capitata* C(3); *Nothria conchylega* F(few), G(1); *Spiophanes kroyeri* C(1), G(2); *Pygospio elegans* C(2); *Polydora concharum* F(1); *Polydora websteri* G(1); *Pherusa plumosa* F(1); *Thelepus cinnatus* C,F,G(many); *Euchone analis* G(1); *Chone duneri* C(many); *Chone infundibulariformis* C(7); *Potamilla neglecta* C(3); *Potamilla* sp. F(several); *Branchiomma* sp. F(2); *Serpula vermicularis* C(many); *Spirobis spirillum* C(many); *Spirobis granulatus* C(many).

SYSTEMATIC LIST OF POLYCHAETOUS ANNELIDS AND COLLECTION STATIONS

APHRODITIDAE

Laetmonice filicornis Kinberg, 1855; 28

POLYNOIDAE

Eunoe oerstedii Malmgren, 1865; 28, 29
Lagisca extenuata (Grube), 1840; 28, 29
Harmothoe imbricata (Linne), 1767; 29
Gattyana cirrosa (Pallas), 1766; 29
Gattyana nutti Pettibone, 1955; 29. NEW RECORD
Austrolaenilla mollis (Sars), 1871; 28
Antinoella sarsi (Malmgren), 1865; 20

SIGALIONIDAE

Pholoe minuta (Fabricius), 1780; 20
Neoleanira tetragona (Oersted), 1845; 28

EUPHROSINIDAE

Euphrosine borealis Oersted, 1843; 29

LOPADORHYNCHIDAE

Pelagobia longicirrata Greef, 1879; 26

PHYLLODOCIDAE

Eteone flava (Fabricius), 1780; 26
Eulalia bilineata (Johnston), 1840; 29
Eumida spp.; 29

SYLLIDAE

Typosyllis fasciata (Malmgren), 1867; 29
Typosyllis armillaris (Müller), 1771; 29
Exogone verugera (Clap.), 1868; 29
Sphaerosyllis sp.; 29
Syllid; 29

NEREIDAE

Nereis pelagica Linne, 1758; 29

NEPHTYIDAE

Nephtys ? incisa Malmgren, 1865; 20
Aglaophamus malmgreni (Théel), 1879; 26

GLYCERIDAE

Glycera capitata Oersted, 1843; 28, 29

SPHAERODORIDAE

Sphaerodorum gracilis (Rathke), 1843; 20, 28

LUMBRINERIDAE

Lumbrineris latreilli (Adouin and Milne-Edwards), 1833; 28
Lumbrineris fragilis (Müller), 1776; 28
Lumbrineris fauchaldi Blake, 1972; 28

ONUPHIDAE

Nothria conchylega (Sars), 1835; 28, 29

ORBINIIDAE

Scoloplos armiger (Müller), 1776; 20
Scoloplos sp. juvenile; 26
Haploscoloplos sp.; 26

PARAONIDAE

- Paraonis gracilis* (Tauber), 1879; 20, NEW RECORD
Aricidea suecica Eliason, 1920; 26

SPIONIDAE

- Prionospio steenstrupi* Malmgren, 1867; 20
Spiophanes kroyeri Grube, 1860; 29
Pygospio elegans Clap., 1863; 29
Polydora concharum Verrill, 1881; 29, NEW RECORD
Polydora websteri Hartman, 1943 juvenile; 29

CHAETOPTERIDAE

- Phyllochaetopterus* sp.; 26

CIRRATULIDAE

- Chaetozone setosa* Malmgren, 1867; 20, 26
Cirratulus cirratus (Müller), 1776; 20

FLABELLIGERIDAE

- Pherusa plumosa* (Müller), 1776; 20
Brada villosa (Rathke), 1843; 26

SCALIBREGMIDAE

- Scalibregma inflatum* Rathke, 1843; 20
Cryptosclerocheilus baffinensis Blake, 1972; 26

MALDANIDAE

- Maldanella davisii* Wesenberg-Lund, 1948; 28
Maldanids; 20, 26

OWENIIDAE

- Myriochele oculata* Zaks, 1923; 20, NEW RECORD
Myriochele heeri Malmgren, 1867; 20, 26

AMPHAERETIDAE

- Melinna elisabethae* McIntosh, 1922; 20
Ampharete arctica Malmgren, 1865; 26, 28
Lysippe labiata Malmgren, 1865; 20
Glyphanostomum pallescens (Théel), 1879; 20, 28
Ampharetids; 20

TEREBELLIDAE

- Polycirrus medusa* Grube, 1855; 20
Thelepus cincinnatus (Fabricius), 1780; 29
Eupolymnia sp.; 28
Pista cristata (Müller), 1776; 26, 28

TRICHOBRANCHIDAE

- Terebellides stroemii* Sars, 1835; 28

SABELLIDAE

- Euchone papillosa* (Sars), 1850; 20, NEW RECORD
Euchone analis (Kroyer), 1856; 29
Chone duneri Malmgren, 1867; 20
Chone infundibulariformis Kroyer, 1856; 29

- Jasmineira schaudinni* Augener, 1912; 26, NEW RECORD

- Potamilla neglecta* (Sars), 1851; 29
Potamilla sp.; 29
Branchiomma sp.; 29

SERPULIDAE

- Serpula vermicularis* Linne, 1767; 29
Spirobis (*Dexiospira*) *spirillum* (Linne), 1758; 29
Spirobis (*Laeospira*) *granulatus* (Linne), 1767; 29

DISCUSSION

The bottom types and depths were different at each of the four benthic stations. These differences were dramatically reflected in faunal composition at each station. Of the 71 species of Polychaeta, only 10 occurred at more than one station. No one species occurred at more than two localities. The following species shared stations: Stations 20 and 26, *Chaetozone setosa*, *Myriochele heeri*; Stations 20 and 28, *Sphaerodorum gracilis*, *Glyphanostomum pallescens*; Stations 26 and 28, *Ampharete arctica*, *Pista cristata*; Stations 28 and 29, *Eunoe oerstedii*, *Harmothoe imbricata*, *Glycera capitata*, *Nothria conchylega*.

The benthic infauna was richest at Station 20, where sandy mud was favorable for grab sampling. Polychaetes were mostly sedentary tube dwellers or burrowers. The dominant species were *Chaetozone setosa*, *Myriochele oculata*, and *M. heeri*. Few polychaetes were retained in qualitative dredge hauls. These samples yielded large numbers of echinoderms, especially asteroids and ophiuroids. One conspicuous asteroid, *Ctenodiscus crispatus*, is a deposit feeder. Molluscs were generally small and few in numbers. This suggests a community structure dominated by infaunal polychaetes and deposit-feeding echinoderms.

The most interesting polychaete collections, from a taxonomic standpoint, come from southern Baffin Bay (Station 26). This locality, in depths ranging from 1745 to 1920 m, yielded one of the two new species and several range extensions. The occurrence of an unknown species of *Phyllochaetopterus* is also of interest as there are no other records of this genus from Arctic waters. Benthic polychaetes were mostly sedentary deposit feeders. The most conspicuous animals were *Cryptosclerocheilus baffinensis*, *Jasmineira schaudinni*, maldanids, and some large alcyonarian corals. Grabs failed to operate in the thick sticky mud. All polychaetes at this station were obtained by qualitative dredge or

from mud which adhered to corners of grabs, shackles, or weights.

Grabs were not used at Station 28 (Davis Strait). Qualitative dredge hauls yielded 17 species of polychaetes. Eleven of these were errantiate, predatory forms, whereas only six were sedentary tube dwellers. The sediment was largely composed of large agglutinated foraminifera. The most abundant polychaete was the predatory onuphid, *Nothria conchylega*.

Station 29 (Little Hellefiske Bank) occurred off western Greenland. Thirty-one species of polychaetes were taken of which 14 were sedentariate. Most of the sedentary species, however, were species which attached their tubes to hard surfaces. The bottom type at this locality was rock and supported large numbers of erect bryozoa; *Thelepus cinnatus* was the dominant polychaete. Grabs were attempted at this station but were jammed by rocks.

Comparisons with other regions: The most extensively studied areas in Arctic and subarctic seas are the western coasts of Greenland, the western Pacific and more recently the Ellesmere Island fjords (Canadian Northwest Territories).

The polychaete fauna off Baffin Island is poorly known as compared with that of western Greenland. The present collections, though sparse, suggest that polychaetes in shallow waters off Baffin Island have remarkable affinities to those occupying similar areas in the western Pacific. No less than 89 percent of the species taken off Baffin Island also occur in the western Pacific (data derived from Ushakov, 1965). This is a greater percentage of shared species than occurs off western Greenland (70 percent shared with the Baffin Island region, data derived from Wessenberg-Lund, 1951). A comparison of the Baffin Island polychaetes with those found by Curtis (1970) in the fjords of Ellesmere Island (N.W.T.), shows that only 53 percent of the Baffin Island species were found by him. This enhances the view that the Baffin Island fauna is indeed rich and deserves more extensive study.

The deeper waters of Baffin Bay also warrant further study. The failure of grabs to operate in the thick clay sediments was disappointing in light of the interesting polychaetes which were taken by qualitative samples. Several transects from the shallow waters of Baffin Island to the deeper waters of Baffin Bay would be desirable and will be planned for future research.

New records and range extensions: The majority of polychaetes taken in this study are widely

distributed in Arctic and boreal seas. Several species were taken which represent new records and range extensions for the areas sampled. Among the more significant are: *Gattayana nutti* and *Polydora concharum*, new to western Greenland (previously known only from Labrador and northeastern America); *Paraonis gracilis*, *Myriochele oculata*, and *Euchone papillosa*, new to the Baffin Island Region (previously known from other circumpolar localities); *Jasmincira schauinslandi*, new to Baffin Bay and areas west of Greenland (previously known from abyssal depths near Spitzbergen, Iceland, and eastern Greenland).

Reproductive biology: Five species were noted to be ovigerous. Eggs were observed in the coelom of *Neoleanira tetragona* and *Euchone papillosa*. *Exogone verugera* contained eggs in a brood sac attached to the abdomen. *Spirorbis spirillum* was brooding eggs in the tube, while *S. granulatus* was brooding eggs in the operculum.

SYSTEMATIC NOTES

The majority of the species encountered are relatively well-known and do not require descriptive comment. *Lumbrineris fauchaldi* and *Cryptosclerocheilus baffinensis* were described earlier (Blake, 1972). Several other species do merit further comment.

FAMILY CHAETOPTERIDAE

Phyllochaetopterus sp.

An anterior fragment from Station 26E (Southern Baffin Bay, 1800 m) measures 10 mm in length. The anterior region consists of 9 segments. There are one or two modified spines on each side of setiger 4. Each spine is brown and terminates in a pointed tooth, which has an excavation on the tip. The species resembles *P. monroi* Hartman, 1967, from the Strait of Magellan. This appears to be the first record of *Phyllochaetopterus* from Arctic seas.

FAMILY OWENIIDAE

Genus *Myriochele* Malmgren, 1867

Synonym: *Galathowenia* Kirkegaard, 1959.

Galathowenia africana Kirkegaard, is herein considered synonymous with *M. oculata* Zaks. The criteria used to distinguish *G. africana* from other oweniids are not sufficient to distinguish

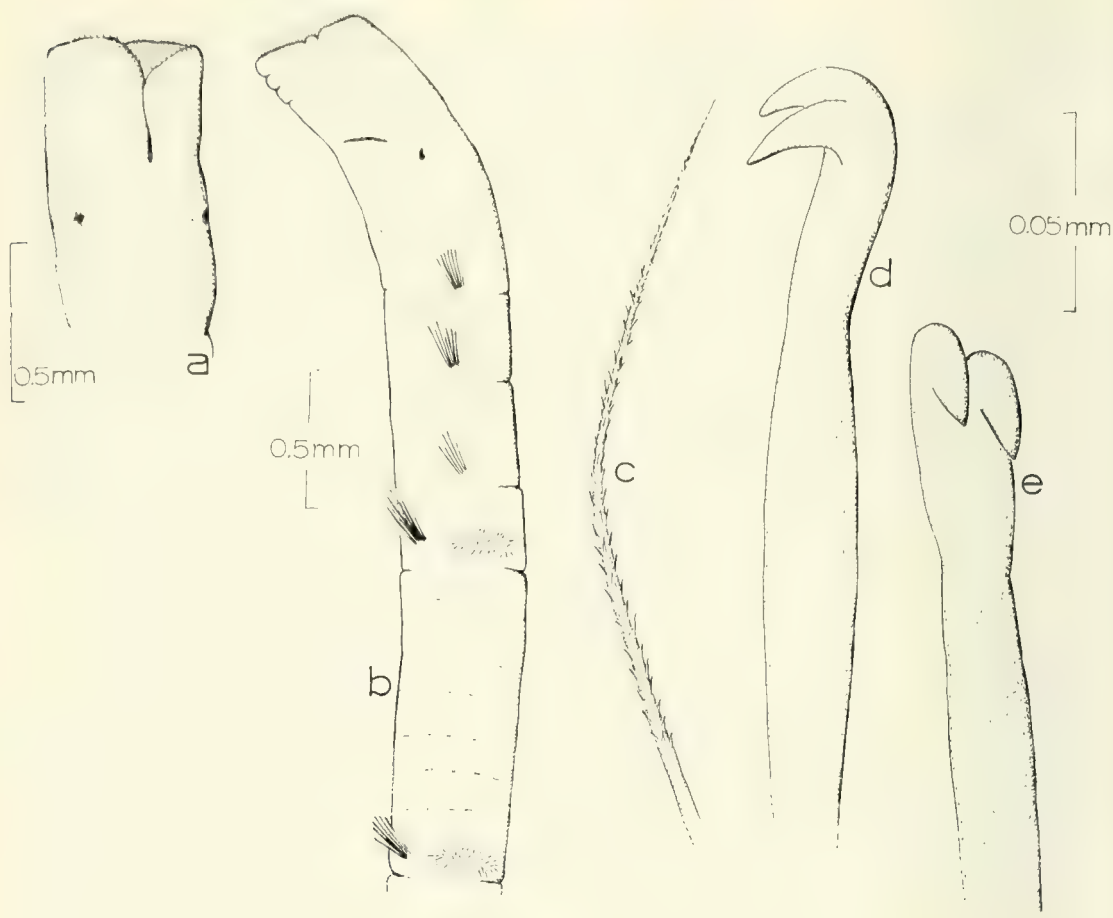


Figure 1. *Myriochele oculata* Zaks, a. head region in ventral view; b. anterior end in lateral view; c. spinous notoseta from setiger 4; d, e. bifid uncinus from setiger 4.

it from *M. oculata*. Kirkegaard's specimens have more pigment, but this in itself is not sufficient for either generic or specific separation.

Myriochele oculata Zaks, 1923

(Fig. 1)

Myriochele oculata Zaks, 1923, pp. 171-174, figs. 1-3; Annenkova, 1937, p. 184; Ushakov, 1950, p. 214; 1955, p. 348, fig. 128h-i; 1965, p. 325, fig. 128h-i.

Galathowenia africana Kirkegaard, 1959, p. 67, fig. 17. NEW SYNONYM.

Numerous specimens were taken at Station 20; length up to 25 mm. The anterior end is truncate, has a midventral cleft but has no cephalic branchiae (Fig. 1a,b). There are two brownish eyes

located on either side of the head. Paired bands of brown pigment are present dorsal to the eyes (Fig. 1b). Occasionally some weakly developed pigment bands may occur ventral to the eyes. All pigment bands may be absent. The head is compressed when the animal is preserved within its tube. If preserved out of the tube, the head is slightly inflated.

The first three segments have notopodial fascicles only; from the fourth, parapodia are biramous with pointed setae in the notopodia and long handled uncini in the neuropodia.

Notosetae are long and spinous (Fig. 1c). Uncini are bifid with the two nearly equal curved teeth, one set slightly higher than the second (Fig. 1d,e). The uncini are small, numerous, arranged in transverse rows and are present in

Myriochele heeri Malmgren, 1867

(Fig. 2)

Fauvel, 1927, pp. 204–205, fig. 71h–m (Synonymy); Wesenberg-Lund, 1950a, pp. 103–104; 1950b, p. 46.

Specimens were obtained from Stations 20 and 26; length up to 22 mm, width up to 1.5 mm. The body is thick throughout, and has up to 30 segments. The anterior end is prolonged and has an anteroventral oral opening. In some specimens the cephalic segment is contracted and the oral opening is more anterior; there are no eyes.

Setigerous segments 1–3 have only notopodial fascicles; thereafter parapodia are biramous. The uncini are long handled and bifid with two teeth, arranged one above the other (Fig. 2b and c). The notosetae are distally multiserrated (Fig. 2a). The posterior end terminates in two weakly developed lateral lobes. A small cirrus protrudes below the anal opening. The tube is composed almost entirely of quartz grains. The species is widely distributed in Arctic boreal seas.

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Figure 2. *Myriochele heeri* Malmgren, a. spinous notoseta from setiger 4; b, c. bifid uncinus from setiger 4.

parapodia to the posterior end. The tube is composed almost entirely of olivine and mica.

The species was previously known from the Sea of Japan, Bering Sea, Chuckchee, Kara, Barents, and White seas; also from west Africa (as *Galathowenia africana*). This is a new record then from Baffin Island.

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ABRASION IN THE MEASUREMENT OF WATER MOTION WITH THE CLOD-CARD TECHNIQUE

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ABSTRACT: Water motion around aquatic organisms produces a significant enhancement of diffusion rates of materials into and out of the organisms. Relative diffusion rates can be determined by measuring the weight lost from immersed CaSO_4 blocks. A comparison of weight lost from CaSO_4 blocks and sediment load along a vertical transect indicated that abrasion was not a significant factor in the loss of weight from the CaSO_4 blocks.

Aside from mass-action effects, water motion around an algal thallus produces a steepening of diffusion gradients, thereby increasing the rate at which materials diffuse in and out (Ruttner, *Naturwissenschaften* 14:1237-1239, 1926). The relationship between current velocity and uptake of phosphate has been described by Whitford and Shumacher (*J. Phycol.*, 1:78-80, 1965) in some detail following their experiments on benthic hydrophytes. However, in most natural situations water motion cannot be adequately described on the basis of current, *i.e.*, velocity, alone.

Relative diffusion rates can be determined by measuring the weight lost from a sparingly soluble material exposed to various conditions of water motion. Independently both Muus (*Sarsia*, 34:61-68, 1968) and Doty (*Botanica Marina*, 14:32-35, 1971) used the dissolution rate of CaSO_4 objects to obtain integrated measurements of water motion over selected time periods.

Muus gave no indication that he was aware of diffusion, as he only stated a concern for velocity. His instruments consisted of CaSO_4 spheres with masses of approximately six gr. Each was mounted on a nail or metal rod. The spherical shape of these instruments allowed for uniform dissolution even though the direction of the water motion might vary significantly. However, the small size of the instruments and the nature of their mounting are inadequate for most field situations we have encountered.

Our concern has been for measuring the enhancement of diffusion rates by water motion over what they would be if the water were motionless at the measurement site. The instruments used (Doty, 1971, fig. 1) for this, called clod-cards, have a mass of about 30 gr. and are roughly rectangular in shape with rounded edges and corners. A piece of nylon "Nitex 300" plankton netting cast in each clod and, protruding from

the bottom and cemented to the card, adds durability to the clod-card preparation. The large size allows exposure periods sufficiently long that short-term variations in water motion will not greatly affect the results. Since the motion often differs so greatly with tide in shallow water marine work the exposure periods are usually near 24 hours, *i.e.*, for a one-day tide cycle. Another advantage of the clod-cards is that they are mounted on rectangular pieces of white matte-finished plastic sheeting. This greatly facilitates labeling the individual instruments and securing them in place in the field.

For both of these instrument types, weight losses indicate rates of dissolution which have been assumed (Doty, 1971) to be essentially due to diffusion, and this would seem certain in less turbulent water. However, the criticism has been voiced that a significant part of the weight loss from such instruments placed in more turbulent water may be due to abrasion from water-borne sediments. To test this hypothesis, an experiment was designed in which a series of clod-cards would be exposed in parallel along with a series of sediment traps.

The sediment traps used were constructed from 16 fluid-ounce aluminum beverage cans. The top of one can was cut off and the bottom used to form the main part of the trap. A 4 cm bottom portion cut from a second can was used to form a lid. A hole one-half inch in diameter was drilled in each end to allow water to pass through. Rubber stoppers (size 00) were used to prevent spillage of samples during handling and storage.

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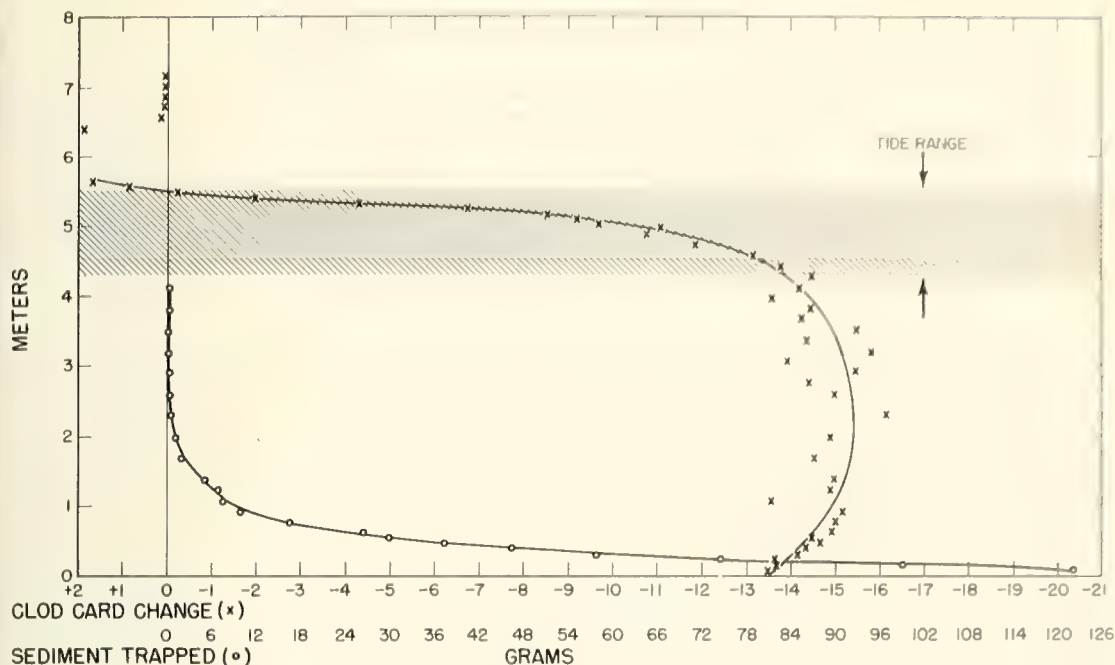


Figure 1. Weight change of clod-cards and amount of trapped sediment plotted as a function depth. Data shown are from one 24-hour exposure period. Above the 4.2 m level, all sediment traps and some clod-cards were damaged by a boat in this run of the experiment. The positions of curves were determined by eye.

The two types of instruments, the clod-cards and the sediment traps, were mounted at intervals along a 24-foot long, 1-inch by 2-inch wooden board. At each interval a sediment trap and a clod-card were fastened on the stringer with masking tape, so that they were opposite one another and at the same elevation. The distance between successive positions was varied to provide a more intense measurement series in certain "critical" segments of the transect. Thus, the intervals were 3 inch for the bottom 2 ft, then 6 inch for the next 2½ ft. The maximum interval of one foot was in mid-water; then, near the surface, the interval was again 6 inch. In use this string of instruments was positioned so the to-and-fro surging motion of the water was parallel to the long axis of the sediment traps and the short axis of the clod-cards. The wooden stringer with the instruments attached was then strapped vertically to a piling on Goleta pier near the Santa Barbara, California, campus of the University of California. Only the more complete of two experiments is described here.

After 24 hours the instruments were retrieved. The weight lost from each of the clod-cards and

the amount of sediment in each of the traps was measured (Fig. 1) and their values compared. The lack of values at several high tide levels was due to a boat having destroyed the instruments there. The clod-card weight increases in the higher intertidal area probably are due to salt deposited from the evaporating of splash or spray.

The amount of water-borne sediment collected was found to be greatest at the bottom and diminished rapidly at successive intervals further from the bottom. Significant amounts of water-borne sediments were found only in the bottom two meters of the transect. Weight losses from the clod-cards, on the other hand, were found to be greatest in the mid-water region and diminished in the bottom two meters.

These results lead us to believe that abrasion is not a significant error-producing factor in the measurement of water motion enhanced diffusion when using clod-cards as the measuring instruments. The financial assistance of U.S. Atomic Energy Commission contract AT(04-3)-235 is gratefully acknowledged.

VARIATIONS IN CONCENTRATIONS OF MAGNESIUM AND STRONTIUM IN RECENT SHELLS OF *TIVELA STULTORUM*

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ABSTRACT: Ten specimens of *Tivela stultorum* from Pismo and Torrance Beaches were analyzed for magnesium and strontium by atomic absorption techniques. Magnesium concentrations in the umbonal areas were consistently greater than those along the margins. Strontium concentrations remained relatively uniform throughout the individual shell. Maximum concentrations were 353 ± 21 ppm for magnesium and 2690 ± 300 ppm for strontium. Minimum concentrations were 114 ± 21 ppm for magnesium and 1770 ± 300 ppm for strontium. Maximum additional magnesium possibly diffused into the shell material of two shells immersed in running sea water for three months was 134 ± 10 ppm. This apparent re-equilibration with sea water suggests that diagenesis can proceed rapidly after death of the animal.

In recent years investigations of skeletal carbonates have been largely confined to relating shell composition to chemical and physical environments. Several relationships have been presented concerning regular variations between different groups of organisms even down to a differentiation between species. If evidence proving that a constant variation within an individual exists, then added importance might be placed on constant chemical variations as useful information to taxonomic grouping and ecological evidence.

The purposes of this study are to examine the changes in concentration of magnesium and strontium within the individuals of the pelecypod, *Tivela stultorum*; to compare two widely separated populations; and to investigate the possible diffusion of magnesium into the skeletal material of the clams upon contact with sea water after death. Studies concerning the deposition of elements under various conditions in the skeletal material of marine fauna may lead to important discoveries with respect to pollution of the environment.

A summary of some of the previous work on this subject will give a background to some of the problems and hypotheses submitted. Chave (1954) concluded that three variables, mineralogy, water temperature, and phylogenetic level are the controlling factors of skeletal magnesium in calcareous marine organisms. Also salinity, depth of water, and age or size of the individual are important factors. He came to three general conclusions applicable to most calcareous marine organisms. First, aragonitic skeletons are lower in magnesium than are those composed of calcite. Second, in all groups a linear relationship exists

between the magnesium in the skeleton and the temperature of the water in which the organism lived. Third, the total amount of magnesium in the skeleton decreases with an increase in phylogenetic level of the organism.

Lowenstam (1954, 1964) has shown that there is a Sr/Ca variation that is temperature-dependent in organisms having the ability to vary their aragonitic content with temperature variations.

Pilkey and Hower (1960) concluded that MgCO_3 content of *Dendraster* tests appeared to be directly related to water temperature and salinity, and that different echinoid species living under similar temperature conditions may deposit substantially different amounts of MgCO_3 .

Harris (1965) determined that only in the case of magnesium is mineralogy a dominant controlling factor in trace element distribution.

Nelson (1967) determined that a heterogeneous distribution of strontium, barium, and manganese within eight species of freshwater clam shells is related to annual growth and shell structure. He also concluded that sodium and magnesium concentrations are relatively constant throughout the shells.

An important paper by Weyl (1967) demonstrated that carbonate minerals in sea water do not behave as homogeneous thermodynamic phases. He concludes that the mineral phase introduced does not come into equilibrium with the solution, but rather, the surface layers of the solid adjust themselves to the aqueous environment.

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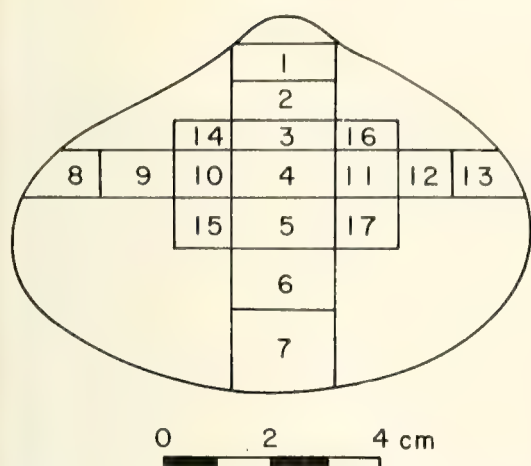


Figure 1. Plan view of a typical shell of *Tivela stultorum* showing the position on each shell used for analysis.

ANALYTICAL METHODS

Sampling method.—Five live clams were collected from each of two California beaches separated by 200 miles of coastline—Pismo Beach and Torrance Beach. All ten clams were collected "in situ." The percent MgCO_3 and SrCO_3 were determined for various parts of each specimen by standard methods of atomic absorption flame spectroscopy using the Perkin-Elmer Model 303 Atomic Absorption Spectrophotometer. From each locality two right valves and two left valves were analyzed. In order to determine accurately any possible trend of variation throughout the shell, the valves were sampled continuously in two perpendicular directions: a) the anteroposterior plane crossing the muscle scars, and b) the plane perpendicular to the growth lines cutting the beak and continuing directly between the muscle scars (Fig. 1). The beak area and dentition were excluded from the analyses due to the complicated structures present in these areas. Thirteen positions were analyzed—seven down and seven across with the center position being common to both directions. On three valves four additional positions were analyzed. Each position was approximately $\frac{3}{4}$ inches square and occupied the thickness of the valve at that particular position. Three clams were also analyzed for variations within the thickness of the valve—a sample was cut parallel and equidistant to the interior and exterior planes, and the interior material was compared with the exterior material.

Analyses.—For each sample three analyses were performed per element. The percent variation of this technique was 13 percent for magnesium and 17 percent for strontium. The four standards used for magnesium in this experiment were 0.2 ppm, 0.5 ppm, 1.0 ppm, and 1.5 ppm. Three standards were used for the strontium analyses—5.0 ppm, 10.0 ppm, and 15.0 ppm.

RESULTS

Magnesium and strontium analyses.—An apparently regular and substantial variation in Mg content is displayed within each of the eight individual clams analyzed. This variation appears to be valid as significant differences in concentration exist with respect to analytical precision. The maximum concentration of magnesium noted in any of the clams analyzed was 353 ± 21 ppm, whereas the minimum concentration was 114 ± 21 ppm. No systematic variation in the strontium content of the shells was noted. The maximum concentration of strontium noted was 2690 ± 300 ppm, whereas the minimum concentration was 1770 ± 300 ppm.

The plane passing directly between the muscle scars and remaining perpendicular to the growth lines from the beak area to the outer edge is referred to herein as the vertical plane. Similarly, the anteroposterior plane crossing the muscle scars is referred to as the horizontal plane. The variations of magnesium in the vertical and horizontal planes of each clam analyzed are shown diagrammatically by the curves in figure 2. A trend can be detected from the concentrations at the respective positions on the shells. An increase in concentration generally appears toward the center of the valve in the umbonal region, and a sharp decrease is evidenced by the decline near the outer margin. A comparison of the Torrance clams with the Pismo clams demonstrates that the Pismo clams do not vary as consistently as the Torrance population. A difference in the average mean concentration between the two populations does not seem to be significant.

A regular variation also appears to exist in the horizontal plane. This variation is somewhat in agreement with the vertical plane distribution as the concentric growth lines appear to have an approximately equal concentration along their respective margins. Also, they appear to give a symmetrical appearance consistent with the growth lines. Standard electron microprobe anal-

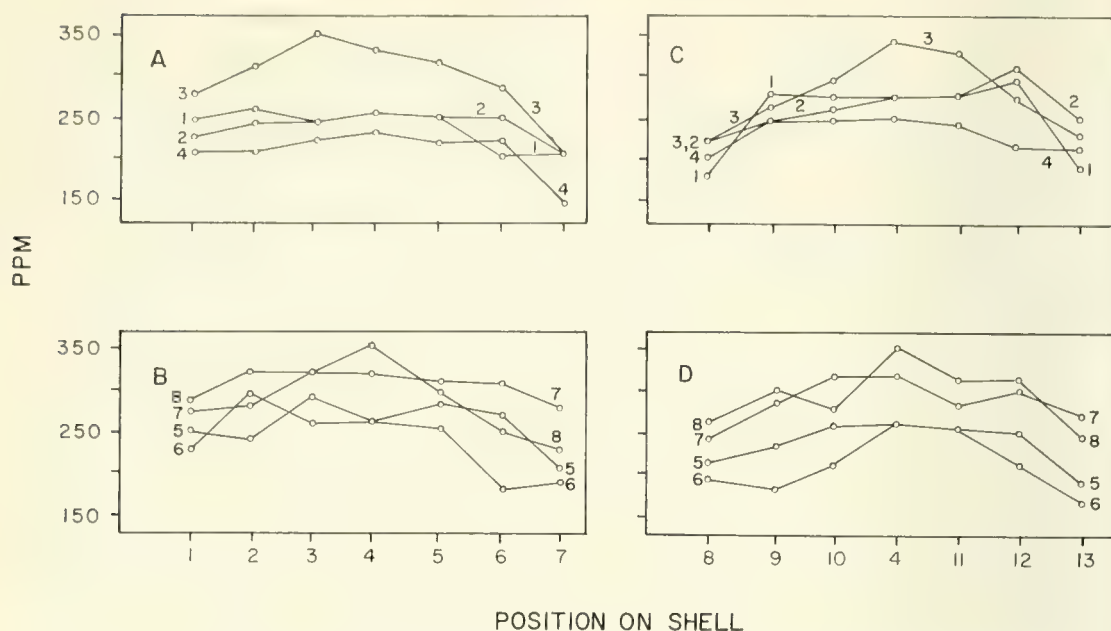


Figure 2. Variation of magnesium in the shell material in two perpendicular directions: A—anteroposterior (vertical) plane—Torrance populations; B—anteroposterior plane—Pismo population; C—horizontal plane—Torrance population; and D—horizontal plane—Pismo population.

yses were conducted on two clams, but no appreciable trends are noted.

Additional analyses were conducted on three clams 3, 4, and 6. Four additional analyses on each gives increased support to the constancy of concentrations along the growth lines. A variation between the nacreous layer and the prismatic layer of the shell is also measureable. It can be seen in table 1 that the nacreous layer of the shell has a concentration much less than the prismatic layer. These values may be the most important values determined, for they may lead to an understanding of the cause of the entire

variation with respect to the skeletal mineralogy and skeletal construction.

Magnesium deposition experiment.—Two additional clams were collected and cut into symmetrical halves, and one half from each clam was placed in circulating sea water in an intake passage of the main tank in Marineland for three months. These shells were then analyzed for magnesium in the same way as the previous samples. Figure 3 depicts the relative uptake of magnesium into the shell material. Only one position on the shell of one of the clams did not reflect a significant uptake of magnesium. The maximum uptake of magnesium noted was 134 ± 10 ppm.

TABLE 1. Comparison of concentrations in the nacreous and prismatic layers for magnesium in position 4 of the clams analyzed.

SAMPLE NUMBER	PARTS PER MILLION
3-N	150 ± 21
3-P	290 ± 21
4-N	180 ± 21
4-P	250 ± 21
8-N	170 ± 21
8-P	270 ± 21

N—Nacreous layer of the shell
P—Prismatic layer of the shell

DISCUSSION

Tivela stultorum grows continuously throughout its life as the shell becomes thicker and increases in diameter (Fitch, 1950). The prismatic layer is secreted by the outer face of the outermost of three lobes at the mantle edge whereas the nacreous layer which does not extend beyond the pallial line is secreted by the general surface of the mantle (Cox, 1969). Timmermans (1969) presents a detailed account of possible mechanisms

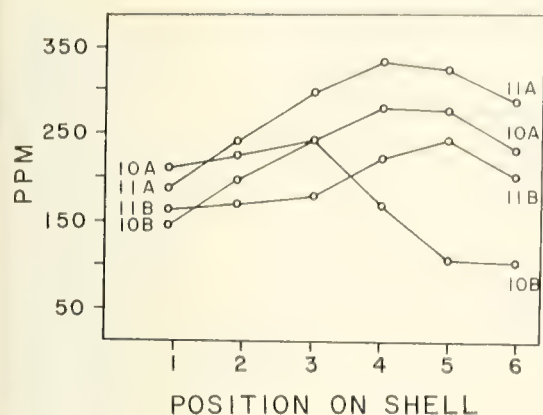


Figure 3. Results of magnesium deposition experiment after three months in circulating sea water. A and B represent the halves of the shells put in sea water for prolonged exposure and those that were not, respectively.

of shell calcification. She concludes that the epithelial regions of the viscera are responsible for secretion of the shell layers including the periostracum and the two calcareous layers in gastropods. An extensive literature exists on deposition of calcium in various genera and species of molluscs.

The prismatic layer thickens from the beak radially, and the nacreous layer thickens in the reverse direction (Fig. 4). Dark colored growth rings commonly present on the shell can be seen distinctly in the Torrance population, but they are lacking in the Pismo population. Their origin is due to a decreased rate of growth in August of each year when the temperature is highest and the seas invariably most calm (Fitch, 1950).

The clams from Pismo Beach display a slight deviation from the Torrance Beach clams in that their mantles overlap the pallial line and extend almost to the shell margin. The exterior layer (Fig. 4) is the prismatic layer, and the interior layer is the nacreous layer. The contact on the interior plane of the valve where the nacreous layer and prismatic layer abut, pinpoints the outermost position where the mantle was attached to the valve.

It has been established by Pilkey and Hower (1960), that $MgCO_3$ content is directly related to water temperature and salinity, and that different species may secrete substantially different amounts of $MgCO_3$ under similar environmental conditions. Harriss (1965), however, proposed that in the case of magnesium, mineralogy is the

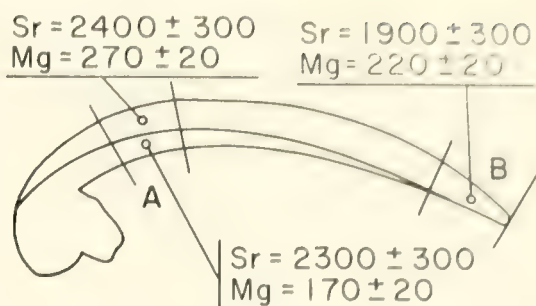


Figure 4. Cross section of clam 8 depicting the relationship of concentration values in ppm at two key positions.

dominant controlling factor in its distribution. He also stated that metabolic processes and crystal growth considerations are of secondary importance with respect to magnesium, but of major importance in strontium distribution. This latter point was initially determined by Odum (1957). He stated that the main factor controlling the Sr/Ca ratio was due to biological differences between groups of organisms. Thus, the main discrepancy in the literature exists between Pilkey and Hower (1960) and Harriss (1965) as water temperature coupled with salinity and mineralogy are the respective arguments for the dominant factor in $MgCO_3$ deposition.

In order to discuss the results of the analyses presented in this paper, the following point must be analyzed. Cox (1969) has shown that alternating layers of conchiolin (a scleroprotein) and aragonite are present in the nacreous layer. The fact that organic compounds may have strontium and magnesium as constituents has been outlined by Dodd (1967). These considerations present a problem which must be solved in order to validate the results presented in this paper. If the conchiolin contains magnesium or strontium which has entered the solution phase in the analyses, then the results of this study will be altered by that factor.

It is possible, however, that a variation of magnesium or strontium may be substantiated if the problem is approached indirectly. The nacreous layer contains much less magnesium than does the prismatic layer, therefore, it would seem that in the outer margin of the shell where the nacreous layer does not exist (Fig. 4), there would be an increase in the magnesium present. Instead, there is a significant decrease. Therefore, a variation in the carbonate material is still a strong possibility. Figure 4 presents a cross-section of clam

8 depicting this relationship. If position A contains a substantial amount of conchiolin in the nacreous material, and since position B belongs entirely to the prismatic layer and contains no conchiolin, then if it is assumed that there is no magnesium in the conchiolin, or if there is, that it is equally distributed and of small concentration, then the expected results should accord a higher amount of magnesium in position B than in position A. The results, however, present the exact opposite. Therefore, if there is no magnesium in the conchiolin as assumed, there would seem to be a variation of magnesium in the aragonitic shell material. The variation of magnesium distribution may occur among the prismatic layers, the nacreous layers, or both.

Dodd (1965) has shown that both magnesium and strontium concentrations vary with respect to the different layers of the specimen, and that a positive correlation between strontium concentration in the prismatic layer and temperature is evidenced while in the nacreous layer a negative correlation with temperature is present. He also has demonstrated that a probable seasonal variation in strontium and magnesium concentrations is shown in the outer prismatic layer in the antero-posterior plane. He has suggested that the cause of the variation between different genera and even between different structural units of the same shell is under strong biochemical control.

Nelson (1967) indicates that a variation between two zones of nacreous layers does exist for freshwater clams. He studied the distribution of trace elements among the annual layers within each of two nacreous zones. He found heterogeneous distribution of Sr, Ba, and Mn within eight species of these clams which he attributed to annual growth and shell structure. A more important aspect with respect to this paper is that he determined magnesium concentrations to be relatively constant throughout the shells. He also reported that there were inherent differences in the trace element composition of clamshells of different species.

This study has revealed that strontium distributions do not seem to vary between the prismatic or nacreous layers of the shell or across the shell to any great degree. Therefore, there may be a similar concentration of strontium in the conchiolin as in the aragonite or an increase of strontium in the nacreous aragonite as opposed to the prismatic aragonite.

In order to determine the magnesium and strontium in the conchiolin, it would be necessary to

separate the organic material from the crystalline material. A procedure is outlined by Degens, Spencer, and Parker (1967). However, even without doing this, the data substantiate a variation of magnesium in the shell material.

Of the variables that have been presented, it seems that salinity and temperature of the water may be responsible for variations across the shell as these factors affected the shell uniformly at the same particular instant in time. It is possible that different secreting cells of the organism are responsive variably with respect to changes in temperature or salinity. It is important to note that since the outer margin of the shell is composed of the youngest shell material, the concentration of magnesium at these positions might reflect a susceptibility of the organism to environmental parametric deviations.

As the shells of *Tivela stultorum* are 100 percent aragonite, it does not seem that the trace element distribution would be controlled by mineralogy. Crystal growth considerations may serve as an important factor in the variation of minor elements since prismatic crystals are deposited perpendicular to the surface, and in the nacreous layer thin leaves of the mineral are oriented almost parallel with the inner surface of the shell (Cox, 1969). This difference may reflect a percent difference in accepting magnesium in the respective components of the shell structure. Magnesium concentration is strikingly less in the nacreous layer than in the prismatic layer as depicted by table 1. If this were a proven variable, the percent $MgCO_3$ would increase toward positions 5, 6, and 7 on each shell.

This analysis of possible variables for the distribution of magnesium in the shell material leaves only one additional known variable which may account for the regular variation of $MgCO_3$ noted in *Tivela stultorum*—metabolic processes.

Considering the possible diffusion of magnesium into the shell material, it is significant to note that the uptake of magnesium may be due to an equilibration of the surface layers of the clams as outlined by Weyl (1967) for carbonate materials in sea water. Ragland, Pilkey, and Blackewelder (1969) support this suggestion as they have shown that Sr/Ca ratios of fossil mollusc shells may be significantly altered by inorganic processes before recrystallization. Lerman (1964) concurs with this in that he implies that concentrations of minor elements in fossil biogenic calcites may be altered by diffusion with no apparent effects in the crystalline texture.

The fact that this diagenesis does occur indicates that post-mortem analysis of shells must be cautiously evaluated until further study determines the degree to which shells have been chemically altered from their original state.

CONCLUSIONS

A variation in the distribution of magnesium in the shell material of *Tivela stultorum* exists, and a constancy of this variation across the shell is apparent. Strontium, however, appears to either remain constant throughout the shell or increase in the nacreous layer. The concentration of magnesium and strontium should be determined in the organic compounds of the nacreous layers of the shells in order to arrive at more conclusive evidence, however, indirectly a variation does appear to exist independent of this factor. The magnesium content is much less in the nacreous layer than in the prismatic layer. Therefore, in spite of the unknown concentrations of magnesium and strontium in the conchiolin, there still appears to be a variation of magnesium in the shell, and this variation appears to stay constant along the growth lines, but decreases from the umbonal area of the valve to the outer margin. From these probable and assumed facts, the following possibilities may exist along with others unknown to the writer. The biological secreting mechanism along with temperature effects may be responsible for the differences in magnesium concentrations in each shell. Mineralogical control and salinity are possibilities that must be explored further. Regardless of the variations of magnesium in the aragonite lattice, however, there is an uptake of magnesium into the shell material of post-mortem shells placed in circulating sea water, and due to this fact, correlations of trace element concentrations of the shells of living animals with fossil shells should be regarded cautiously.

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RESEARCH NOTES

SPECIES GROUPS OF NORTH AMERICAN CHORUS FROGS (GENUS *PSEUDACRIS*: FAMILY HYLIDAE)

Seven species of chorus frogs are currently included in the North American genus *Pseudacris*: *Pseudacris brachyphona*, *P. brimleyi*, *P. clarki*, *P. nigrita*, *P. ornata*, *P. streckeri*, and *P. triseriata*. These seven species have been divided into different intrageneric groups by different authors. The most recent designation was that of Chantell (Amer. Midl. Nat., 80:381-391, 1968), who divided the extant species into two groups: the *ornata* group containing *P. clarki*, *P. ornata*, and *P. streckeri*; and the *nigrita* group containing *P. brachyphona*, *P. brimleyi*, *P. nigrita*, and *P. triseriata*. Based on the data reported in the present paper, I propose that this scheme be changed by transferring *P. clarki* from the *ornata* group to the *nigrita* group.

During the course of a detailed study of the complete skeletons of the 32 species of tree frogs found in the temperate regions of the northern hemisphere, I examined entire and disarticulated skeletons of specimens from the seven species listed above. Each specimen was cleared in 2 percent potassium hydroxide, stained with alizarin red S, and dehydrated and stored in glycerine. The following number of specimens of each species were studied: *P. brachyphona*, 7; *P. brimleyi*, 2; *P. clarki*, 5; *P. nigrita*, 4; *P. ornata*, 7; *P. streckeri*, 3; and *P. triseriata*, 5.

The following species groups can be established solely on the basis of osteological data; the *ornata* group containing *P. ornata* and *P. streckeri*; and the *nigrita* group containing *P. brachyphona*, *P. brimleyi*, *P. clarki*, *P. nigrita*, and *P. triseriata*.

The *ornata* group can be diagnosed in the following way (the contrasting character state found in the *nigrita* group is given in parentheses): 1) a solid articulation is present between the nasal bone and the facial spine of the maxilla (Fig. 1) (no nasal-maxillary articulation); 2) nasals are elongate and deeply notched laterally (nasals sub-triangular and not laterally notched); 3) a flattened process projects from the anterior arm of the septomaxilla (no anterior septomaxillary process); 4) more than 30 percent of the frontoparietals are involved in the frontoparietal-sphenethmoid articulation (less than 30 percent); 5) a solid articulation is present between the palatine bones and vomerine tooth patches (no palatine-vomerine articulation); 6) vomerine tooth patches are relatively large (vomerine tooth patches are relatively small); 7) anterior extension of vomer is directed toward the anterior end of the maxilla (anterior vomerine extension is directed toward posterior end of premaxilla); 8) more than 30 percent of the

anterior arm of the parasphenoid overlaps the sphenethmoid (less than 30 percent); 9) the posterior lateral arms of the parasphenoid are less than 20 percent of the length of the anterior arm (more than 20 percent); 10) the horizontal arm of the squamosal is reduced and horizontal arm length/vertical arm length less than 50 percent (well developed horizontal arm, horizontal arm length/vertical arm length = more than 80 percent); 11) the quadrate is calcified (quadrate is cartilaginous); 12) the clavicles are thickened, especially medially (Fig. 2) (clavicles thin and narrow); 13) coracoids are directed posteromedially (coracoids directed medially); 14) pectoral fenestra is relatively large and rounded (pectoral fenestra relatively small and elongate); 15) deltoid ridge of humerus is pierced longitudinally on its ventral surface by a groove and foramen (no groove or foramen); and 16) the ventral acetabular expansion of the ilium is relatively small (relatively large expansion).

The above osteological character states are found in adult individuals and, even though some of them represent differences in degree and not in kind, it is very easy to distinguish members of the two species

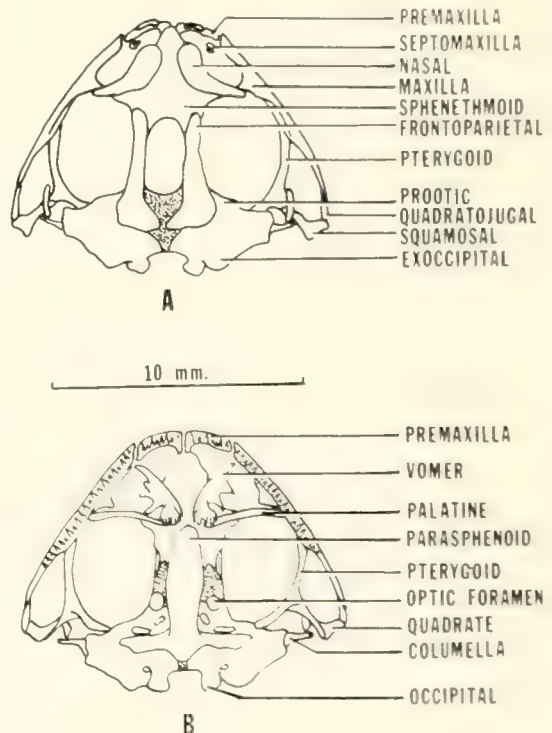


Figure 1. The skull of *Pseudacris streckeri* in dorsal view (A) and ventral view (B).

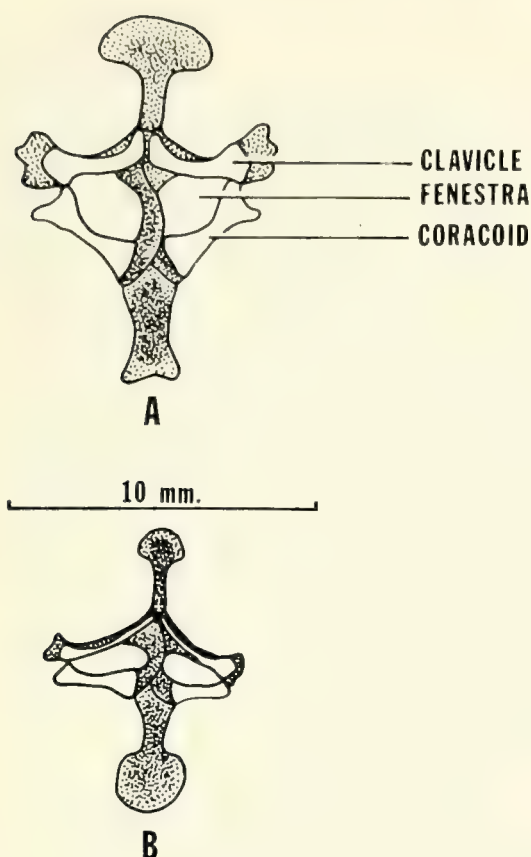


Figure 2. Ventral views of the pectoral girdles of *Pseudacris streckeri* (A) and *Pseudacris clarki* (B).

groups from one another when one examines their skeletons.

In general, the skeleton in specimens from the *ornata* group is more developed than that in specimens from the *nigrita* group. In the former, the anterior end of the head is compact with two solid lines of articulation. Dorsally, the nasals provide a bony bridge joining the lateral maxillae solidly with the medial sphenethmoid. Ventrally, the palatines serve as transverse braces connecting the maxillae, sphenethmoid, and vomers. The arrowhead-shaped sphenethmoid is proportionately larger in size in the *ornata* group and involves much of the medial edges of the nasals in an overlapping articulation. The prootic and exoccipital ossifications are extensive and occupy much of the otic capsule.

By way of contrast, the cranial ossifications in the specimens examined from the *nigrita* group are not as extensive (Fig. 3). The posterior end of the nasal capsules is not as heavily supported by bone, nor do the ossifications in the otic capsules develop as extensively.

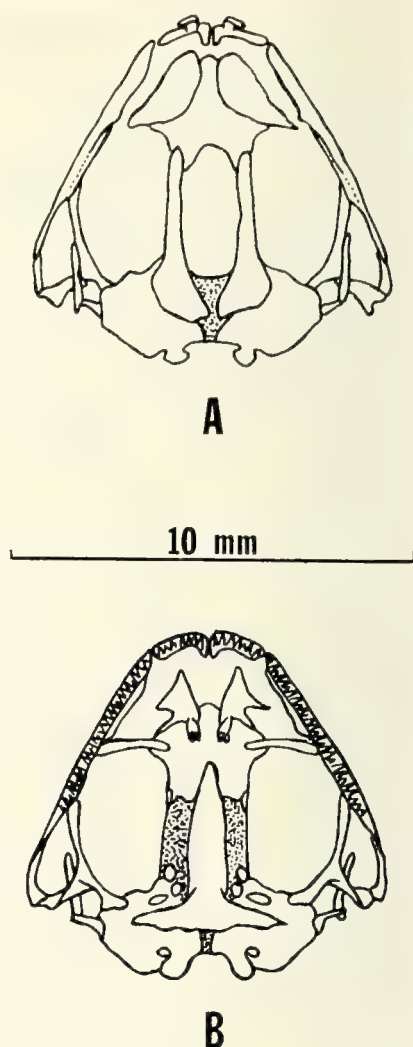


Figure 3. The skull of *Pseudacris nigrita* in dorsal view (A) and ventral view (B).

An examination of the external morphology of specimens of the seven species of *Pseudacris* suggests the same intrageneric division indicated by a comparative study of their skeletons. Species in the *nigrita* group are smaller in size and resemble one another in general appearance. *Pseudacris ornata* and *P. streckeri* are stout bodied forms whose limbs are also more massive than those in the species of the *nigrita* group.

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THE OS TRANSILIENS IN FOUR SPECIES OF TORTOISES, GENUS *GOPHERUS*

Ray (1959), first found a heterotropic or sesmoid bone, the os transiliens, in a chelonian, *Gopherus polyphemus*. Legler (1962) discovered the presence of the os transiliens in *Gopherus agassizi* and *Gopherus flavomarginatus*.

Ray (1959) showed histologically that the os transiliens in *Gopherus polyphemus* was bone and not calcified cartilage. Differential stains of toluidine blue (for cartilage) followed by alizarin red S (for bone) were carried out on a series of 20 os transiliens taken from *Gopherus agassizi* and *Gopherus berlandieri* (Evans, 1949; Willey, 1969).

X-rays were taken of the os transiliens and compared to known samples of bone and cartilage in *Gopherus agassizi* as a check upon the determination of the presence of bone. A General Electric model 11AA-3A X-ray machine was used at 40 KVP and 50 milliamps using Kodak Industrial type M-2 X-ray film.

Carapace length, skull length, and length and width of the os transiliens were measured on nine *Gopherus agassizi*, one *Gopherus polyphemus*, and two *Gopherus berlandieri*. Skull length was measured in a straight line from the anterior extremity of the snout to the tip of the supraoccipital crest with the skull resting on the articulated mandible. The greatest width and length of the os transiliens were measured. The length of the carapace was measured along the midline between vertical axes erected at the posterior border of the supracaudals and the anterior border of the nuchal.

The movement of the os transiliens was examined on seven thawed and two live *Gopherus agassizi*, using a wire and x-ray analysis technique developed by Inman (1947).

The os transiliens is a prow-shaped bone in the aponeurosis of the *M. adductor mandibularis externus* and is articulated in a joint capsule with a facet formed by the quadrate and prootic bones, the *processus trochlearis oticum* (Gaffney, 1972). This facet places the os transiliens slightly higher on its inner surface and somewhat lower on its outer lateral surface. The os transiliens appears to provide a gliding or smooth motion for the fan-shaped aponeurosis of the *M. adductor mandibularis externus* over the edge of the superior temporal fossa where it passes ventrally to an insertion on the mandibular coronoid process.

The os transiliens of all adult *Gopherus agassizi* (15) showed positive stains for bone. Five juvenile *Gopherus agassizi* showed positive stains for cartilage suggesting a replacement of cartilage by bone with maturity. The differential staining technique also indicated the presence of a small bony os transiliens in one specimen of *Gopherus berlandieri* which is the first to be so noted. The x-rays confirmed the staining data in all cases.

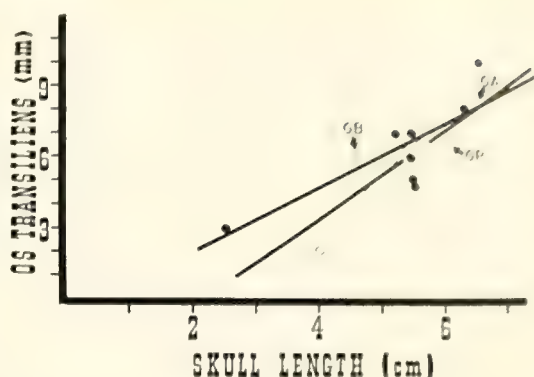


Figure 1. Skull length (cm) relative to the left os transiliens length (mm) in *Gopherus agassizi* (dots), *Gopherus polyphemus* (open circles), and *Gopherus berlandieri* (open squares). The relationship between the os transiliens and skull length for *Gopherus agassizi* was found by the method of least squares to be $Y = 1.42X - 1.18$ and for *Gopherus polyphemus* to be $Y = 1.85X - 3.90$.

Ossification of the os transiliens occurs at a smaller size in *Gopherus agassizi* than has been found in *Gopherus polyphemus* (Fig. 1). The size of the os transiliens compared to carapace length in *Gopherus agassizi* (Fig. 2) shows that the larger tortoises have proportionally larger os transiliens (Table 1).

In *Gopherus agassizi* the superficialis portion of the *M. adductor mandibularis externus* contracts and pulls on the broad part of the fan-shaped aponeurosis attached to the upper end or posterior portion of the os transiliens. This is adducted (inside the joint capsule) posteriorly on the process trochlearis pulling on the tendon attached in part to the front of the os

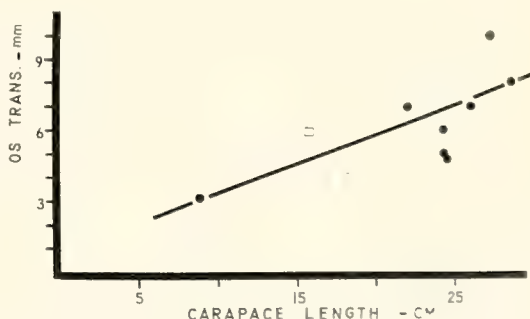


Figure 2. Carapace length (cm) relative to length of the left os transiliens (mm) for *Gopherus agassizi* (dots), and a single specimen each of *G. polyphemus* (open circle), and *G. berlandieri* (open square). The relationship between the os transiliens and carapace length for *Gopherus agassizi* was found using the method of least squares. The relationship is $Y = 0.259X + 0.33$.

TABLE 1. Correlation coefficients between carapace length, skull length and os transiliens; A, *Gopherus agassizi* and B, *Gopherus polyphemus*.

(r_{xy})	A	B
between os and skull length	0.801	0.940
between os and carapace length	0.742	—
between skull and carapace length	0.927	—

transiliens and in part to the belly of the superficialis portion of the *M. adductor mandibularis*. This tendon pulls, ventrally, on the coronoid process thereby pulling the mandible up which in turn closes the mouth. No evidence was found for any involvement of the outer lateral edge of the *M. adductor mandibularis* (Fig. 3), in *Gopherus agassizi* as had been suggested for *Gopherus polyphemus* by Ray (1959). Ray (1959) had also suggested (based solely upon preserved specimens) that the os transiliens might act as a means of providing a longer lever arm for the action of the jaw closing musculature or as some sort of buttress for the muscle to pull against. It appears instead, that the os transiliens serves only as a means of providing a smooth or gliding action for the jaw musculature over the superior temporal fossa as shown by x-ray analysis.

It thus appears that the os transiliens is probably found in all members of the genus *Gopherus* and develops in cartilage which is subsequently replaced

by bone. It also appears that the os transiliens ossifies earlier in young individuals of *Gopherus agassizi* than in other species studied. The os transiliens seems to be a device to smooth the translation of the horizontal pull of the *M. adductor mandibularis* ventrally in pulling the mandible shut.

I wish to thank Bayard Brattstrom and James Smith for their assistance in this study and for reviewing the manuscript.

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RATE OF HEAT LOSS BY LARGE AUSTRALIAN MONITOR LIZARDS

Bartholomew and Tucker (1964) have shown that there is a difference in the rate of heating and cooling in Australian monitor lizards. They implicated vasomotor and respiratory mechanisms to explain this difference. The availability of several large Lace Monitors, *Varanus varius*, some more than twice the size used by Bartholomew and Tucker, allowed the testing of one of these mechanisms.

Four large monitor lizards were used in a series of heating and cooling experiments where core (cloacal and esophageal), deep (10-28 mm) and shallow muscle, and skin surface temperatures were monitored continually. Temperature readings were taken at irregular intervals using a Yellow Springs Instrument

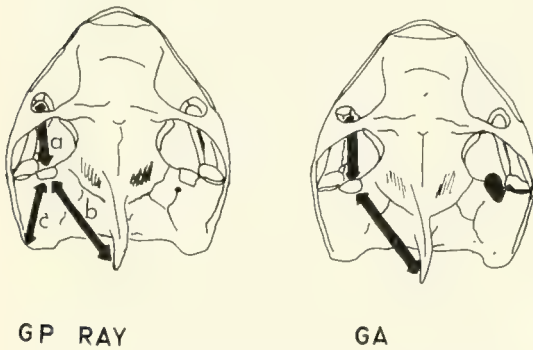


Figure 3. Comparison of suggested muscle action of *M. adductor mandibularis externus* in closing the jaw as suggested by Ray for *Gopherus polyphemus* (GP) and the present study for *Gopherus agassizi* (GA). The dark area on the right side of the *Gopherus agassizi* skull shows the relative position of the os transiliens. The symbols used in the figure include: a. tendon of *M. adductor mandibularis externus*; b. posterior belly of *M. adductor mandibularis externus portio superficialis*; c. posterior belly of the *M. adductor mandibularis externus portio profunda*.

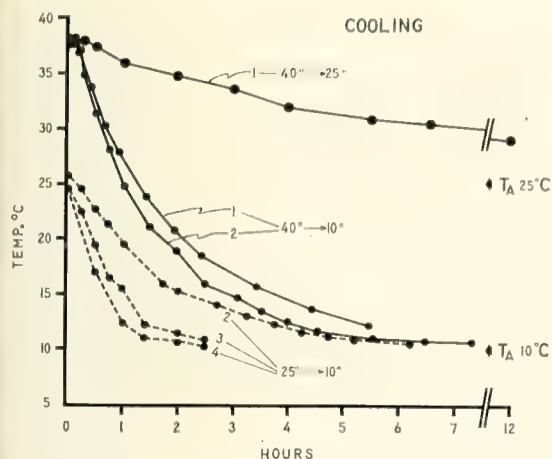


Figure 1. Body temperatures (cloacal) of Lace Monitor lizards, *Varanus varius* of various sizes upon cooling from 40° to 25°, from 40° to 10°, and from 25° to 10°C. Lizard 1 is the largest, 4 is the smallest; see text for measurements and weights.

Co. Telethermometer Model 44TD, 0–50°C and thermister probes. All probes were calibrated against a US Bureau of Standards Certified thermometer. Deep cloacal and esophageal temperatures were taken with #402 vinyl, ensheathed probes; skin surface temperatures with banjo probes; and subdermal and muscle temperatures with various sizes of hypodermic probes. Autopsy showed no significant or extensive hemorrhaging about the hypodermic probes. Head length, snout-vent length, tail length (mm), and weight (gms), respectively, for the four lizards used in this study are as follows: No. 1, 133, 765, 1149, 10,400; No. 2, 125, 676, 1129, 7,850; No. 3, 98, 535, 835, 2,563; No. 4, 67, 365, 645, 510. Lizard number one was the largest in size and weight. Lizards 1, 2, and 3 were captured in Victoria and 4 was obtained in Queensland. The lizards had been kept in captivity for between four weeks and a year and were in good condition. Lizards 1 and 4 had heavy layers of ventral fat. The lizards were not fed for at least three days prior to tests. Each lizard was tied to a wire frame two feet above a table so that air circulated all around the lizard. Though restrained, the depth of breathing did not seem impaired. The test lizard was placed in a large constant temperature room that maintained a temperature with $\pm .2^\circ\text{C}$. Blowers which circulated air within the room passed air over and around the lizard at an average rate of 640 ft/min. After reaching the temperature of one room, the rack, lizard with imbedded probes, and telethermometer were quickly transferred to another constant temperature room.

As expected (Fig. 1) the rate of cooling depends both upon the temperature differential between the lizard and the environment and with size; larger lizards losing heat slower than the smaller lizards.

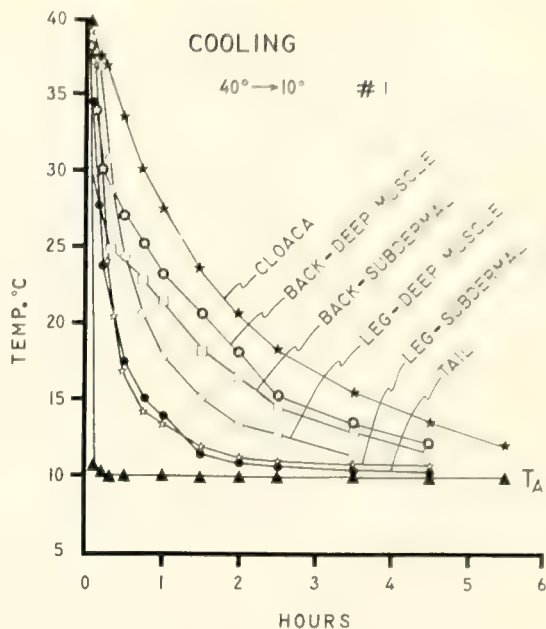


Figure 2. Cooling curve for Lace Monitor No. 1 from 40° to 10°C, showing differences in tail, leg, muscle, and cloacal temperatures.

Smaller lizards, of course, heat up faster than large lizards regardless of whether they are placed in a warm ambient temperature or are under heliothermic basking conditions (Bartholomew and Tucker, 1964; Cowles, 1958; Bartholomew and Lasiewski, 1965).

Figure 2 shows the cooling curve for Lace Monitor No. 1 transferred from 40° to 10°C. Tail and leg temperatures drop quickly to ambient temperatures, whereas deep body temperatures take more than 6 hrs to reach ambient. Esophageal temperatures were almost the same (or 0.2°C cooler) as cloacal temperatures. Figure 3 shows similar data for lizard No. 2 transferred from 25° to 10°C. Tail temperatures drop rapidly, back muscle, back subdermal, and deep abdominal (not shown in Fig. 2) are intermediate between tail and cloacal temperatures. Shielded (with masking tape) back skin surface temperatures were similar to subdermal, while side-skin surface temperatures were intermediate between subdermal and tail temperatures.

The rapid drop of the tail and leg temperatures to ambient and the slower drop of the core temperature to ambient (up to 7 hrs) suggests that when cooling the Lace Monitor lizard may be shunting blood from the appendages to the center of the body. In one experiment, the temperature of the tail was taken at several points along its length. All tail temperatures dropped at about the same rate, suggesting that the effect is not just that of a counter-current heat exchange system or just due to differences in the physical dimensions of different parts of the tail.

The temperatures shown in figures 2 and 3 show

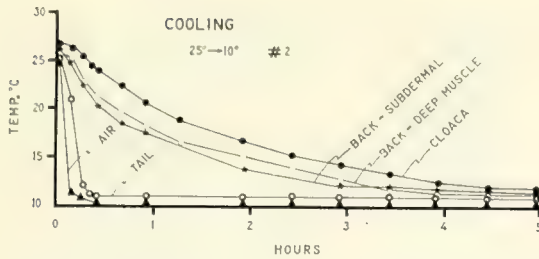


Figure 3. Cooling curve for Lace Monitor No. 2 from 25° to 10°C, showing the rapid drop in tail temperature and slow drop in cloacal temperature.

a gradient of temperature from outside to core rather than any bands of temperature or any core and shield differences. Autopsy revealed that the peripheral body muscles of monitors are few and thin; a condition similar to most other lizards. There was no dorsal or lateral fat, though ventral fat was present. Thus the skin of the monitor does not appear to be very effective in reducing heat loss.

Slow cooling rates have been reported for several reptiles (Cowles, 1958; Cogger and Holmes, 1960; Bartholomew and Tucker, 1964; Mackay, 1964; Bartholomew and Lasiewski, 1965; Bartholomew, 1966; Myres and Eells, 1968; Stebbins and Barwick, 1968). Stebbins and Barwick (1968) showed that monitor lizards often spend the night in tree-hole retreats. This behavior plus the data presented herein suggests that in such retreats (where there is less wind than in the experimental condition) the body temperatures of the monitors would probably not reach ambient until morning. This would facilitate nocturnal digestion of foods eaten during the day as well as reducing the heating time of the lizard in the morning.

Though most reptiles are ectothermic, a small amount of internal endothermic heat production is possible. This amount is usually so small that it is immediately lost to the environment, hence it does not contribute to body temperature. Surface-volume relationships would suggest that in large reptiles a small amount of heat production plus a reduced rate of heat loss could contribute to body temperature. Bartholomew and Tucker (1964) calculated that at 25°C a monitor lizard might add 2°C to its body temperature by endogenous heat production. The large lizard used in the studies reported herein was stimulated for five minutes under an ambient temperature of 25°C (body temperature 25°C). In this experiment, the lizard raised its body temperature 2°C (to 27°C, but no higher) due to the increased muscular activity. When stimulated at an ambient temperature of 10°C no rise in body temperature could be detected.

Heat retention and a reduction in thermal conductance are both enhanced by larger body size and reduced surface area. Large Galapagos tortoises thus show little internal daily fluctuation in body tem-

perature (Mackay, 1964). Dinosaurs presumably would have had even less of a daily fluctuation in body temperature. Further, vasomotor control of rate of heat loss may be another physiological mechanism used by reptiles to control and modify their body temperature and may also be an important step towards the development and evolution of homeothermy and endothermy.

This work was carried out during an NSF Senior Postdoctoral Fellowship (56017) in the Department of Zoology and Comparative Physiology, Monash University, Clayton, Victoria, Australia. I wish to thank James W. Warren and A. K. Lee for their kindnesses and Lucien Vandeveld, Mike Owen, and John Nelson for collection, use, care, and assistance with these large lizards.

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COVER: A new species of brachyuran crab from deep water off Peru. Its genus, *Acanthocarpus*, which was not previously known from the west coast of the Americas, is characterized by the long, transverse spine on the merus of each cheliped.

Illustration by Jerry J. Battagliotti, University of Southern California.

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THE SYSTEMATIC STATUS AND DISTRIBUTION OF COSTA RICAN GLASS-
FROGS, GENUS *CENTROLENELLA* (FAMILY CENTROLENIDAE),
WITH DESCRIPTION OF A NEW SPECIES

PRISCILLA H. STARRETT AND JAY M. SAVAGE¹

ABSTRACT: The glass-frogs (Family Centrolenidae) of Costa Rica comprise 13 species all placed in the genus *Centrolenella*. A review of the *fleischmanni* group indicates that six species: *C. fleischmanni*, *C. colymbiphyllum*, *C. chirripoi*, *C. valerioi*, *C. talamancae*, and *C. vireovittata*, a new species, from southwest Pacific Costa Rica, occur in the republic. Salient features for distinguishing the species include head structures and proportions, degree of tympanum development, finger webbing, color patterns and male calls. The nominal taxa *C. chrysops* Cope, *C. decorata* Taylor, and *C. millepunctata* Taylor, are placed in the synonymy of *fleischmanni*; *C. reticulata* Taylor is regarded as a synonym of *C. valerioi*. Detailed distributional analysis for all 13 Costa Rican species of the genus indicates that most forms occur in lowland or premontane slope evergreen forest. As many as six or seven species may occur at the same locality, although few species show consistent co-occurrence at many sites. No obvious ecologic factor explains the diversity and differences in species composition from site to site. The mosaic distributional pattern and a similar unique mosaic of basic and derived features distinguishing each species makes determination of relationships within species groups difficult. Within the *fleischmanni* line, *chirripoi*, *talamancae*, and *fleischmanni* appear closely allied. *Centrolenella vireovittata* resembles this stock in basic coloration and male call but is unique in the family in having a striped dorsum. *Centrolenella valerioi* and *C. colymbiphyllum* do not appear to be closely related to any other forms, although the two may be included with *vireovittata* as a subgroup based upon characteristics of the head and snout region.

Among the most characteristic inhabitants of riparian situations along small fast-moving streams in tropical Middle America, are a series of small, delicate, pale green arboreal frogs allied to *Centrolenella fleischmanni* (Boettger) of the glass-frog family (Centrolenidae). We have discussed elsewhere (Savage, 1967; Savage and Starrett, 1967) the salient features of Central American glass-frog species belonging to the *prosoblepon* and *pulverata* groups of the genus *Centrolenella* and take this opportunity in describing a new Costa Rican form to review the members of the *fleischmanni* group in the region.

Frogs of this group are small (22–27 mm in standard length in adults) elusive creatures with males that call from vegetation overhanging the stream by night and with both sexes hiding by day, well-camouflaged by their coloration, among

the leaves of streamside plants. In many areas, including vacant lots within some of the large cities, these frogs are extremely common among stands of ginger-lilies (Family Zingiberaceae: especially *Costus* and *Hedychium*), in and around small streams or even rivulets of only a few millimeters in depth. Members of the group share the following features (egg color not known for all species): no vomerine teeth; white bones; a colorless parietal peritoneum so that the viscera are visible through the transparent abdominal skin, in life; white visceral peritoneum; liver confined by white hepatic peritoneum to form a compact bulb-shaped organ rather than

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the large three-lobed structure characteristic of most other centrolenids; dorsum pale green fading to whitish-yellow in preservative; no humeral hooks; no enlarged forearm muscles in males; no free prepollex or prepollical spines; eggs green, in life, white in preservative (Starrett, 1960) and are usually attached to the under surfaces of leaves overhanging water courses. The green pigment in the eggs is obvious when they are in the oviduct and at the time of laying. As cleavage takes place, the developing embryo becomes whitish-yellow but the yolk retains a greenish cast for some time.

Taylor (1958) in the most recent survey of the situation, recognized nine Costa Rican species belonging to the *fleischmanni* group. Together with the Mexican form *C. viridissima* (Taylor) this makes a total of ten nominal species for Middle America.

Although we regard some of these forms as conspecific, the small size (19–27 mm in standard length), few distinguishing features and subtle differences between closely allied taxa, make identification of preserved material extremely difficult. Familiarity with the animals in life in the field is an absolute prerequisite to any attempt to clarify the status of these frogs, particularly as the significant features of dorsal coloration and the distribution of guanine on the heart and viscera may best be determined in life. Fortunately we have collected and seen living examples of all nominal forms except *C. chirripoi* and *talamancae*. Nevertheless, we hold no belief that this review is a final word on the group in the region. It is however the best that can be done on the basis of preserved material and current field observations. Further resolution of possible problems must await intensive field study with emphasis on male call characteristics. Such studies may reveal the presence of cryptic sympatric species at several localities.

We encourage herpetologists to undertake further field study of the following problems:

1. The status of the *fleischmanni* population of southeastern Atlantic slope Costa Rica with moderately large yellow dorsal spots and an indistinct but evident tympanic apparatus; the relationship of this population may be with *C. talamancae* which has a more fully evident tympanum and more protuberant nostrils than the *fleischmanni* population.

2. The possible occurrence of a form with the morphology of *fleischmanni* but with a call similar to *valerioi* at Los Diamantes, Provincia de Limón, Costa Rica.

3. The presence of a diminutive (adult males 19–

20 mm) form with a distinctive weak *fleischmanni*-like call from near San Isidro de El General, Provincia de San José, Costa Rica.

4. The possible sympatric occurrence of two species of reticulated frogs, all here referred to *C. valerioi*, from the Peninsula de Osa, Costa Rica.

5. The possible sympatric occurrence of frogs similar to *C. talamancae* with *colymbiphylum* and *fleischmanni* in the Cordilleras Tilarán and Central of Costa Rica.

GENERAL CHARACTERISTICS

The following features are common to the species of the *fleischmanni* group treated in this report: upper surfaces smooth; nostrils directed laterally; eyes directed forward at about 45° angle to body axis; eye membranes opaque; orbit round; pupil of eye horizontally elliptical; undersides of palms and fingers covered by low smooth tubercles; fingers with lateral fleshy margins; disks rounded to truncate, slightly wider than fingers; thenar tubercle obscure, narrow and elongate; palmar tubercle small rounded; subarticular tubercles moderate; no webbing between fingers I–II; underside of foot smooth; toe disks small, rounded; a weak elongate inner metatarsal tubercle, no outer; subarticular tubercles small; modal toe webbing formula I 1½–2 II 0–2 III 1–2¼ IV 2½–1 V; throat smooth; venter and posterior ventral areas of thighs granular, rest of undersides smooth; choanae large, ovoid; ostia pharyngia moderate; tongue oval, small; paired vocal slits and a single external vocal sac in males.

In all species of this group for which eggs are known (*colymbiphylum*, *fleischmanni*, *talamancae*, and *valerioi*) the eggs are green but become white upon preservation. Egg color is unknown for *chirripoi* and *vireovittata*. Other centrolenids from Costa Rica having green eggs are *C. spinosa* of the *prosoblepon* group and *C. pulverata* of the *pulverata* group. The eggs of *C. albomaculata*, *C. euknemos*, and *C. granulosa* contain much melanin and appear dark (black or brown) and white in the oviduct or shortly after laying. The eggs of *C. prosoblepon* are black and *C. ilex* probably has black eggs as well, since the oviducal eggs are black in the holotype.

POPULATIONAL DIFFERENCES

Head Structures and Proportions: Among the most distinctive qualitative features distinguishing among the members of this group are the outline of the head viewed from above, the snout profile,

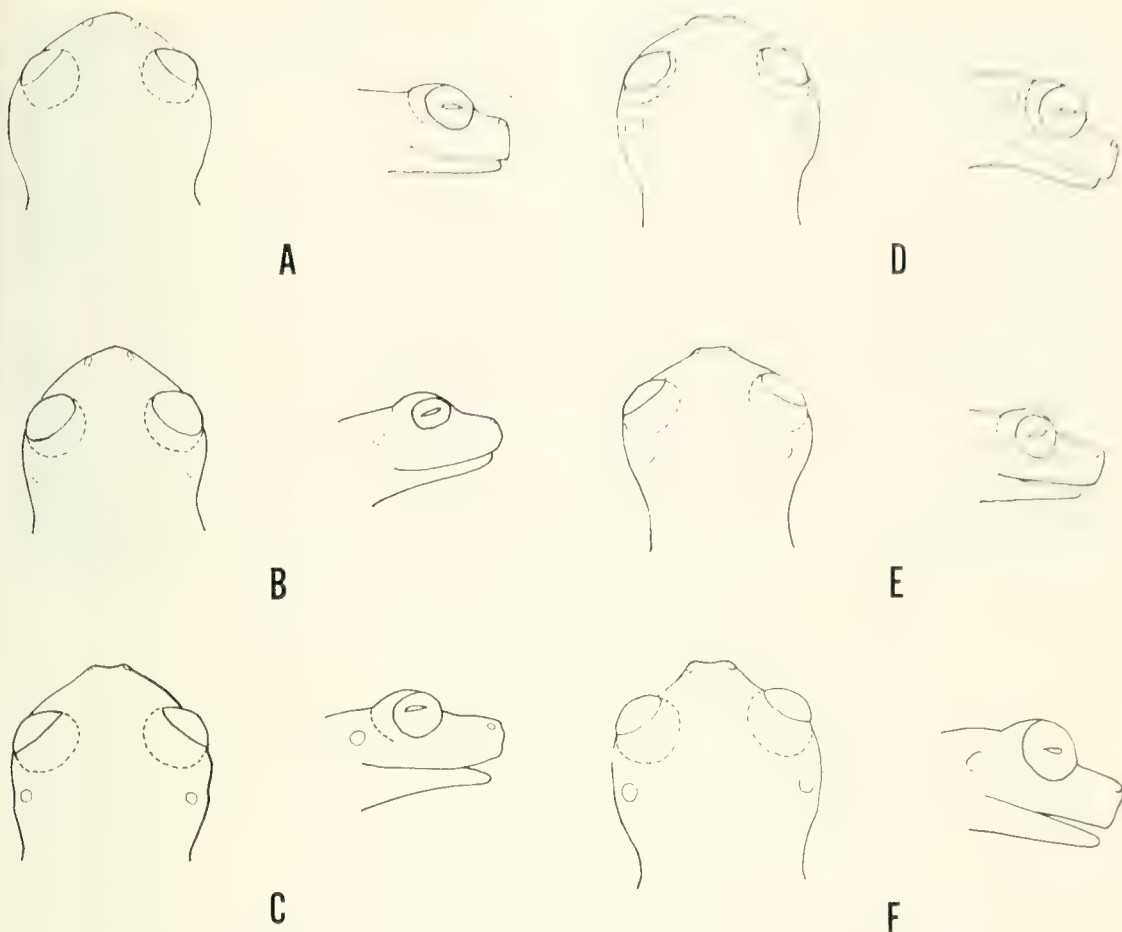


Figure 1. Diagnostic features of head structures and proportions in Central American species of glass-frogs of the *fleischmanni* group. Dorsal and lateral views, A. *Centrolenella fleischmanni*, B. *C. talamancae*, C. *C. chirripoi*, D. *C. vireovittata*, E. *C. valerioi*, F. *C. colymbiphyllum*.

the structure of the canthal and rostral regions, including the degree of development of raised nasal protuberances, the extent to which the eye protrudes laterally, past the margin of the lip, and the relative proportions of the interorbital and loreal (eye to nostril) regions.

When viewed from above the head outline may be semicircular with a truncate (Fig. 1E) or slightly indented (Fig. 1D), rounded with a slightly indented rostral area (Fig. 1C) or truncate with an indentation between the nostrils (Fig. 1F) or rounded with a weakly pointed tip (Fig. 1A–1B). In lateral view the snout is rounded (Fig. 1B) or vertical (Fig. 1E) in profile. In some forms each canthus rostralis is strong and the elevated area between them forms a distinct platform terminating with the

nostrils (Fig. 1D–1F). In others the canthus is weak and no platform is developed (Fig. 1A–1C). The nostrils open through very slightly indicated fleshy areas (Fig. 1A) in some forms. In others the nasal region is markedly swollen and the nostrils open through elevated fleshy protuberances that lie on distinct raised ridges (Fig. 1B–1F).

The eyes, when not retracted extend laterally only slightly beyond the lip margin in most forms (Fig. 1A–1E) but in one species the eyes extend laterally far beyond the lip margin to provide a pop-eyed effect (Fig. 1F).

The relative proportions of the loreal (eye to nostril distance) to least interorbital width may also be used to characterize samples. The term loreal short refers to samples in which the loreal



A



B

Figure 2. Pericardial pigmentation in live glass-frogs of the *fleischmanni* group. A. white parietal pericardium; ventral view of *Centrolenella valerioii*; B. Colorless parietal pericardium; ventral view of *C. colymbiphyllum*. Former, courtesy of W. E. Duellman; latter, courtesy of R. W. Merritt.

distance is less than the interorbital; loreal long is used for forms in which the loreal distance equals or exceeds the interorbital width.

Tympanum: Dunn (1931) and Taylor (1954) pointed out differences in the degree of external evidence of the tympanum as a basis for distinguishing among centrolenid species. In most centrolenids (*i.e.*, members of the *pulverata* and *prosoblepon* groups in Costa Rica, Savage, 1967; Savage and Starrett, 1967) the tympanic membrane is evident although covered by a thin layer of integument and the tympanic annulus is distinct and demarcates the tympanic area. Within the *fleischmanni* group, some species have the tympanum distinct with the tympanic annulus clearly indicated as above. In others the tympanum and annulus, while present, are concealed beneath a thick portion of the integument and are only faintly indicated. In this discussion, the term tympanic apparatus distinct (Fig. 1C, 1E, 1F) and tympanic apparatus concealed (Fig. 1A) refer to each of these conditions respectively. In one form (Fig. 1B) the tympanum is evident but indistinct and is intermediate between the previously described extreme conditions.

Webbing: In all but one species considered in the present report there are no more than vestigial webs at the base of fingers between fingers I–II–III, but the web between fingers III–IV extends at least to the level of the penultimate subarticular tubercle of both digits. The modal finger webbing formula for these forms following the system of Savage and Heyer (1967) is I 3–3 II 3–3 III 1½–2 IV. In *Centrolenella chirripoi*, the webbing between fingers II–III is almost as extensive as between fingers III–IV and the species has a modal finger webbing formula of: I 3–3 II 1¾–2½ III 2–2 IV.

Peritoneal and Pericardial Pigmentation: In all members of this group the venter and parietal peritoneum are transparent in life so that the internal organs are visible. In addition, most of the digestive organs are covered by white visceral peritoneum. The presence of the white hepatic peritoneum is absolutely correlated with the occurrence of a compact bulb-like liver in all specimens of this group studied in life or shortly after preservation. Although we have seen no fresh examples of *Centrolenella chirripoi*, or *C. talamancae*, these forms have the bulb-

like liver typical of the *fleischmanni* group and surely have similar peritoneal pigmentation. In the *prosoblepon* group of centrolenids, the liver is clearly three-lobed. *Centrolenella pulverata* agrees with members of the *fleischmanni* group in liver form and in having a white hepatic peritoneum. In most species the heart is enclosed in a similarly colored white sac (Fig. 2A) the parietal pericardium, so that the heart appears as a white organ in life. Several other species, including the new form, lack white pigment in the pericardial sac, so that the heart appears red (Fig. 2B) in life. Careful dissection of well-preserved animals will usually show whether the heart is protected by white pigment or not, although very old examples or those exposed to strong formalin or light may lack the pigment even if it were present in life. Since the heart or pericardial sac is visible through the ventral skin in life, these differences are valuable field characters for identifying certain species and should be recorded at the time of capture.

Dorsal Color Pattern: The available evidence indicates that at least two chemically distinctive pigments are involved in the green coloration of Central American centrolenids. In members of the *prosoblepon* group, the green dorsal color of the live frog comes from a pigment concentrated in a dense system of chromatophores. After a short time in formalin or alcohol this pigment appears purple and the animal seems purple to lavender in color to the unaided eye. In frogs that have been in preservative for a long time or exposed to light, the purple changes to brown. The pigment that appears to be purplish after preservation in this group is hereafter called pigment A. Dried skins of fresh examples of the *prosoblepon* group that have not been fixed in preservation change from green to purple after a short time.

In most members of the *fleischmanni* group the green dorsal color of live frogs is produced by widely scattered chromatophores containing a pigment that turns to purple, or with a long period in preservative to brown, that we assume is pigment A, and a suffusion of green pigment that covers most of the dorsal surfaces. The latter pigment, hereafter called pigment B, is soluble in formalin and alcohol. In frogs of this group, the green rapidly disappears after preservation and they appear a uniform yellowish-white to the unaided eye. Closer examinations reveal that the body is covered by widely scattered chromatophores that appear to be purple to

brownish and contain pigment A. Dried skins of fresh examples of this group that have not been fixed in preservative resemble preserved examples. In one species of this group, *C. valerioi* (Fig. 3D), pigment B is concentrated in the form of a broad reticulum mixed with melanophores. Upon preservation, the green pigment dissolves but the melanophores continue to indicate the extent of the reticulum.

A third pigment may be involved in the coloration of *C. pulverata*. In life, the dorsal green coloration of this frog is formed by widely scattered chromatophores and a diffused green pigment that covers most of the skin area. In preservative the chromatophores change to purple and we assume they contain pigment A. The diffuse pigment dissolves in formalin or alcohol so that to a superficial view, the animal appears to be yellowish-white, but because of the fairly numerous chromatophores containing pigment A, the color has a pale lavender cast. Whether the diffuse soluble green pigment of *pulverata* corresponds to pigment B is questionable, since dried skins of fresh examples that have not been fixed in preservative remain a bright green with scattered purple chromatophores.

Goin and Goin (1968) and Barrio (1965) provide a partial explanation for this situation through their studies of coloration in hylid and pseudid frogs. According to the Goins, the green color of hylids and probably some centrolenids that appear purple in preservative is a structural color. In this case three layers of chromatophores are involved. The deepest are melanophores, more superficial are guanophores and near the skin surface are the lipophores. In life, when visible light falls on the skin, the shorter wave length components (greens, blues, purples) are reflected back by the guanophores and the longer wave length components (reds, oranges, yellows) are absorbed by the melanophores. As reflected the shorter wave lengths pass through the lipophores and the blues and purples are mostly absorbed while the greens are transmitted so that the skin appears green. On preservation, the fatty yellow materials in the lipophores are dissolved or destroyed and the reflected blues and purples are transmitted and the skin appears purplish. If this is indeed the situation in centrolenids, pigment A is guanine.

In centrolenids of the *fleischmanni* group pigment B is almost certainly biliverdin (Goin and Goin, 1968; Barrio, 1965) a green pigment

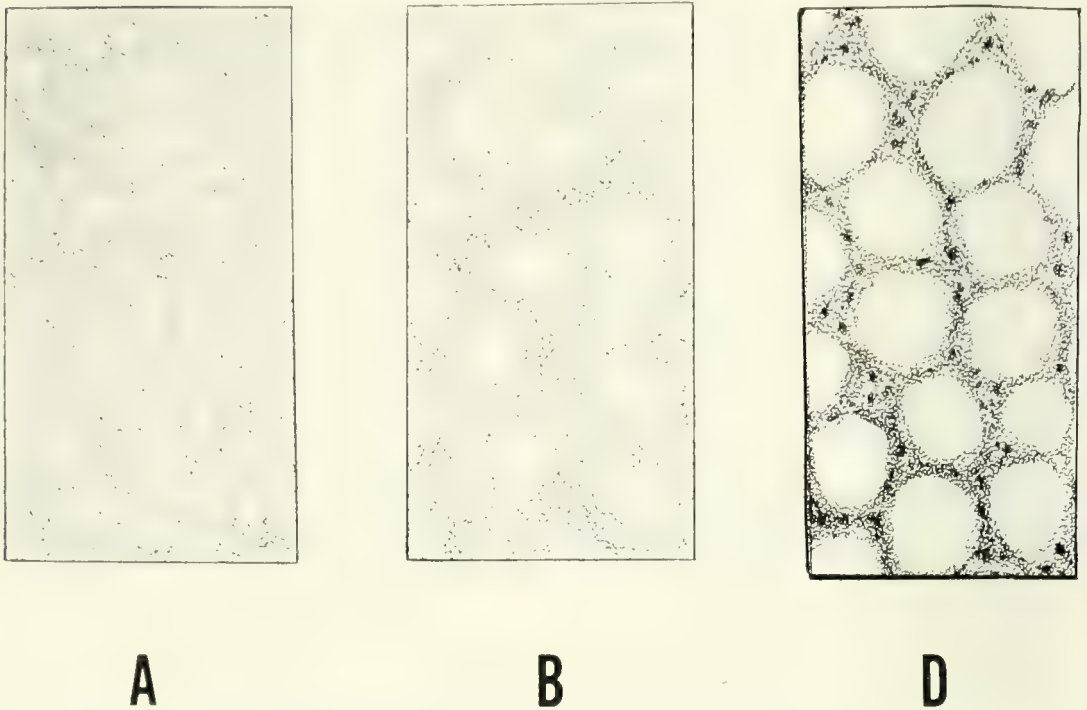


Figure 3. Diagrammatic representations of basic dorsal color patterns in *Centrolenella fleischmanni* and its allies. The letters (A,B,D,) refer to the pattern types discussed in the text.

that is accumulated in the skin rather than in chromatophores. On preservation the biliverdin-like pigment in centrolenids is dissolved or destroyed so that the skin appears pale yellow or white, although scattered purplish (pigment A) and black (melanophores) chromatophores may be present. Another diffuse green pigment besides biliverdin may be present in the skin of *C. pulverata*, since the pigment is not destroyed when the skin is dried.

Barrio (1965) found biliverdin in bones, muscles, eggs, and lymph of several hylid and pseudid frogs. Although it has not been biochemically verified, the green pigment in the eggs of members of the *fleischmanni* group and in the bones of species of the *prosolepon* and *pulverata* groups of centrolenids is probably biliverdin. It is interesting to note that in the *fleischmanni* group, the skin and eggs contain the green pigment, while in the *prosolepon* group, the green pigment is concentrated in the bones, but not in the skin or eggs. In *C. pulverata*, the green pigment is in both skin and bones but is much less concentrated than in the

skin of *fleischmanni* and its allies or in the bones of members of the *prosolepon* group.

In life, all members of the *fleischmanni* group have a pale leaf green ground color with some light yellow markings. In preservation the yellow disappears and the green fades until the frog appears almost uniform yellowish-white on casual observation. Closer examination under magnification usually shows that the green pigmentation is still indicated by scattered contracted purplish or in examples that have been preserved for a long time, brownish chromatophores. Several patterns occur that distinguish several species (Figs. 3, 5):

A—dorsum appears almost uniform green in life, but with many small yellow spots; in well-preserved specimens the light areas seen under a microscope correspond to the yellow spots, but because of the contraction of the dark chromatophores are larger in area than the spots in life;

B—dorsum green in life with moderate-sized yellow spots; in well-preserved specimens the spots are indicated as in A above, with the same qualifications;

C—dorsum green in life, with a distinct green mid-dorsal stripe bordered on either side by a para-

vertebral yellow stripe; remainder of dorsum and flanks with moderate-sized yellow spots; in well-preserved examples the mid-dorsal stripe is indicated by contracted dark chromatophores and the light para-vertebral stripes by pigmentless areas; the remainder of the dorsum resembles the situation in pattern B above;

D—in life the dorsal ground color appears to be a pale yellow to bright yellow-gold; superimposed on the light ground color is a regular broad reticulum composed of many black punctations suffused with a pale green; in some populations the green suffusion extends over the yellow areas surrounded by the reticulum so that they appear as a murky chartreuse; the large light spots apparently correspond to the yellow spots in the other patterns (A, B, C); these light areas are usually at least one-half the eye diameter in pattern D and often are as large as the eye; in preservation the green is completely dissolved but the dark punctations of the reticulum are retained and the pattern is visible to the unaided eye; under magnification the reticulum is seen to be composed of a series of purplish to black chromatophores (brown in some examples that have been in preservative for a long time).

Male Vocalizations: During the rainy season male centrolenids call nearly every evening. The calls seem to be related to both spacing of the males and courtship of the females. The calls of males in the *fleischmanni* group consist of single notes repeated after a pause of several seconds. Three distinctive calls are known for this group (Fig. 4). In *C. valerioi*, the note is of short duration (0.2 sec.) and is a rather high pitched seet. In *C. fleischmanni* and the new species, *C. vireovittata*, the sound resembles a rising whistled wheet, is lower pitched and lasts for 0.4–0.5 sec. The most distinctive call is the long trilled musical call (0.6–0.8 sec.) of *C. colymbiophyllum*. Unfortunately the calls of *C. chirripio* and *C. talamancae* remain unrecorded.

Other Features: Taylor (1954) emphasized a number of other features as a basis for recognizing species within the group. Review of his material and our extensive samples from throughout Costa Rica indicate that these characteristics vary individually or interpopulationally to such a degree that they cannot be relied upon for species recognition.

Eye tunic color—in centrolenids, the outer surface of the eyeball, posterior to the cornea, is covered by a thin membrane that underlies the eyelids. In life this membrane or eye tunic contains a heavy concentration of guanine. Upon preservation as the green pigments of the integument fade, the eye tunic pigment may be seen

through the upper eyelids as a definite white area. Taylor (1954) noted that in preservative some individuals lacked the white tunic area and he used this difference as a basis for separating several nominal species. The presumed differences (white versus black eye tunics) are artifacts, for upon preservation and depending upon the nature and time of death, strength of preservative, exposure to light and other factors, the white pigment may disappear and the area seen through the upper eyelid appears black from the color of the eyeball. In all members of the *fleischmanni* group seen by us in life, the guanine is present in the eye tunic. After death some individuals in any large sample lose the white color, while others retain it for years.

Terminal digital pads—Taylor (1954) described two pad conditions for this group: a) rounded, distinctly wider than adjacent part of digit; b) truncate or subtruncate, not or only a little wider than adjacent part of digit. Careful examination of series from single localities indicates that these features are variable within a population, with most individuals having intermediate conditions.

Thigh folds—three examples within Taylor's large series of *fleischmanni* have a pair of skin folds that run from the vent laterally and downward on the thighs. Five frogs within our samples from widely scattered localities show similar folds formed by a wrinkle in the thigh integument. The folds are not present in living frogs and appear to be an artifact of preservation, caused by the simultaneous swelling of the skin and its separation from the underlying muscle and flexing of the thighs during the death throes.

STATUS OF NAMED MIDDLE AMERICAN FORMS

Centrolenella fleischmanni

The earliest available name for Costa Rican frogs of this group is *Hylella fleischmanni* Boettger, 1893 (holotype: Senckenberg Museum 3760, Provincia de San Jose: San Jose, 1180 m). This form is represented in our collections by numerous specimens from San Jose and the immediate vicinity. Most of the animals called *Centrolenella fleischmanni* (Noble, 1924) *Centrolene fleischmanni* (Dunn, 1933), *Cochranella fleischmanni* (Taylor, 1951, 1952, 1958) and *Centrolenella fleischmanni* (Goin, 1964) belong here, although it is difficult to separate poorly preserved material from the allied *Centrolenella talamancae*.

Centrolenella fleischmanni may be briefly charac-

terized as follows: 1) head viewed from above, rounded with a weakly pointed tip; 2) snout truncate in profile, loreal short; 3) canthus rostralis weak, no elevated intercanthal platform; 4) nostrils open through very slightly indicated fleshy areas; 5) eye not protuberant; 6) tympanic apparatus concealed; 7) reduced webbing between fingers I–II–III, but web between fingers III–IV well-developed; 8) parietal pericardium white; 9) dorsum green with small to moderate yellow spots; 10) male call a single rising untrilled wheet, repeated after a pause.

Cope (1894) described *Hylella chrysops* from Alajuela and San Jose, Costa Rica and Taylor (1954) revived the name for *fleischmanni*-like frogs from near Sarchi, Provincia de Alajuela and Provincia de Cartago, Costa Rica. The sole nominal difference between *chrysops* and *fleischmanni*, according to Taylor is the presence of a black eye tunic in the former and a white tunic in the latter. Since this difference is an artifact of preservation as pointed out above and since our extensive material indicates that only one species resembling *fleischmanni* occurs on the Meseta Central Occidental of Costa Rica, we regard the two forms as conspecific. The types of *chrysops* are lost and in order to assure the stability of our conclusion, we herewith designate Senckenberg Museum 3760, the holotype of *Hylella fleischmanni*, as the neotype of *Hylella chrysops*.

Taylor (1942) differentiated *Centrolenella viridissima* (holotype: FM 100093, Mexico: Guerrero: Agua del Obispo) from *C. fleischmanni* of Chiapas on the basis of slight mensural differences and eye tunic color (black in the former, white in the latter). Duellman (1960) concluded that all Mexican material represented a single species, that the characteristics used by Taylor were variable in Mexico and overlapped to a considerable extent with series of Costa Rican *fleischmanni*, but tentatively recognized *viridissima* as distinct. We can find no basis for separating *viridissima* from *fleischmanni* particularly as the Mexican and Costa Rican samples are connected by a continuous series of populations ranging through Guatemala, El Salvador, Honduras, and Nicaragua. The name *viridissima* is based upon a population having the parietal pericardium silvery white as in all *fleischmanni* and cannot be confused with the populations here referred to *C. colymbiphyllum*, which have the pericardial sac colorless.

Cochranella decorata Taylor, 1954 (holotype: KU 36896, Costa Rica: Provincia de Cartago: Hacienda La Florencia, 4.8 km SW Turrialba, 800 m) was recognized as distinct solely on the basis of having prominent skin folds on the posterior thighs lateral to the vent. In addition to the holotype, Taylor referred two examples (KU 36883–84, presumably from Costa Rica: Provincia de San Jose: San Jose, 1180 m) to this species. We have examined the types and five additional Costa Rican examples (Provincia de Alajuela: Candelaria de Naranjo, CRE 525, 2 specimens; nr. Carrizal, CRE 6037; Provincia de San

Jose: La Palma, CRE 503, 2 specimens) with the thigh folds and conclude that the folds are artifacts of preservation, as noted above. All eight examples agree in every other respect with typical *fleischmanni* taken at the same localities and we refer *C. decorata* to the synonymy of the latter form.

Cochranella millepunctata Taylor, 1954 (holotype: KU 36887, Costa Rica: Provincia de San Jose: La Palma, 1500 m) was distinguished from *fleischmanni* by its describer by having the terminal digital pads enlarged, distinctly wider than adjoining part of digits (versus digital pads truncate or subtruncate, not or only a little wider than adjoining part of digit in *fleischmanni*). As noted above the shape of the terminal pads varies from rounded to truncate in samples of *fleischmanni* from single localities. The holotype and paratypes all from Costa Rica (topotypic examples: KU 36883–86, 36888–94; KU 36897 from Provincia de Alajuela: Sarchi and KU 23943 probably from Provincia de Cartago: Moravia de Chirripo) seem to represent the extreme rounded and expanded pad condition but other examples from the same localities have subtruncate to truncate pads and many are intermediate between the extreme conditions. For this reason we regard *millepunctata* as a synonym of *C. fleischmanni*.

Centrolenella fleischmanni, as conceived of in this report, has a broad geographic and altitudinal range: lowlands and premontane slopes in humid areas from Guerrero and Veracruz, Mexico, south through Central America to western Ecuador and through northern Colombia and Venezuela to Surinam.

Centrolenella colymbiphyllum

In Costa Rica, *C. fleischmanni* is sympatric at a number of localities with another small form that resembles it superficially both in life and in preservative. The earliest name for this second species is *Centrolenella colymbiphyllum* Taylor, 1949 (holotype: KU 23812, Costa Rica: Provincia de Heredia: Isla Bonita 1200 m). *Centrolenella colymbiphyllum* may be distinguished by the following series of characteristics: 1) head viewed from above truncate with an indentation between nostrils; 2) snout truncate in profile, loreal long; 3) canthus rostralis strong, with an elevated intercanthal platform; 4) nasal region markedly swollen and nostrils opening through elevated fleshy protuberances that lie on distinct raised ridges; 5) eyes protruding laterally well beyond level of margin of lips; 6) tympanic apparatus distinct; 7) reduced webbing between fingers I–II–III, but web between fingers III–IV well-developed; 8) parietal pericardium colorless; 9) dorsum green with small to moderate yellow spots; 10) male call a single sustained trill, repeated after a pause.

Centrolenella colymbiphyllum occurs in Costa Rica in humid areas of the premontane zone on both slopes of the Cordillera de Tilaran, on the Atlantic slope of the Cordillera Central and extreme north-

eastern extensions of the Cordillera de Talamanca; the species has also been taken in Pacific lowland forests from the area just west of San Isidro de El General in the Golfo Dulce region of southwest Pacific Costa Rica. *Centrolenella colymbiphyllum* may have a substantially broader geographic range than suggested by Costa Rican samples. Specimens of *fleischmanni* allies lacking white pericardial pigment have been noted from Guatemala, Honduras, Panama, and Venezuela and some of these frogs may be referred to the present species after detailed study.

Centrolenella chirripoi

Taylor (1954) also described another distinctive species apparently related to both *fleischmanni* and *colymbiphyllum*, but closest to the former, as *Cochranella chirripoi* (holotype: KU 36865, Costa Rica: Provincia de Limón: Río Cocolis, near Suretka, 100 m). Examination of the holotype and eight topotypic paratypes indicates that this form is a valid species that may be characterized as follows: 1) head viewed from above rounded with a slightly indented area between nostrils; 2) snout rounded in profile, loreal long; 3) canthus rostralis weak, but with an elevated intercanthal platform; 4) nasal region markedly swollen and nostrils opening through elevated fleshy protuberances that lie on distinct raised ridges; 5) eyes not protuberant; 6) tympanic apparatus distinct; 7) webbing between fingers II–III–IV extensive; 8) color of parietal pericardium not known; 9) dorsum green with small to moderate yellow spots; 10) male call not known.

Centrolenella valerioi

Dunn (1931) described another distinctive *fleischmanni* ally from Costa Rica as *Centrolene valerioi* (holotype: MCZ 16003, Costa Rica: Provincia de San José; La Palma, 1370 m). Because the original description implied that the only two known examples, the holotype and a topoparatype (MCZ 16005), had a distinct narrow mid-dorsal stripe, Taylor (1954) failed to recognize the species among his materials. Re-examination of the type specimens of *valerioi* proves it to be conspecific with examples of a species of *Centrolenella* with a dorsal pattern of green reticulations on a light yellowish ground color. The "mid-dorsal green stripe" mentioned by Dunn corresponds to the portion of the green reticulum that tends to coalesce down the back in this form. Dunn (1933) later associated the types of *valerioi* with examples of the reticulate form from Panama: Cocle: El Valle de Anton and emphasized the "green chain markings" of the types. This species may be characterized by the following: 1) head viewed from above semicircular, with a truncate or slightly indented tip; 2) snout truncate in profile, loreal long; 3) canthus rostralis strong, with an elevated intercanthal plat-

form; 4) nasal region markedly swollen, with nostril opening through elevated fleshy protuberances that lie on distinct ridges; 5) eyes not protuberant; 6) tympanic apparatus distinct; 7) reduced webbing between fingers I–II–III, but web between fingers III–IV well developed; 8) parietal pericardium white; 9) dorsal pattern of large yellow spots surrounded by a strong reticulum of green pigment and dark punctations; 10) male call a single short note, repeated after a pause.

Cochranella reticulata Taylor, 1954 (holotype: KU 32922, Costa Rica: Provincia de Cartago: near main bridge over Río Reventazón, at Instituto Interamericano de Ciencias Agrícolas, Turrialba, 591 m) is a strict synonym of *C. valerioi*. It was also recorded by Taylor from Costa Rica: Provincia de Cartago: Moravia de Chirripo; Provincia de Heredia: Cariblanco; Provincia de Limón: Suretka; Provincia de Puntarenas: Golfito, Palmar.

The reticulated species, *C. valerioi*, is known from the Atlantic foothills and slopes of the Cordillera Central of Costa Rica south along the margin of the Cordillera de Talamanca to the lowlands of the Valle de Talamanca near the Panama boundary; it also occurs on the Pacific versant in lowland sites from near San Isidro de El General south through southwestern Costa Rica to El Valle de Anton in central Panama.

Cochranella talamancae Taylor, 1952 (holotype: KU 4143; Costa Rica: Provincia de Cartago: Moravia de Chirripo, 1116 m) is an enigmatic form. According to Taylor (1952; 1958) the species is closely allied to *C. valerioi* but re-examination of the type and three additional examples (KU 32936–38) referred to *talamancae* by Taylor (1958) do not support this concept. Salient features of this series are: 1) head viewed from above, rounded with a weakly pointed tip; 2) snout rounded in profile, loreal short; 3) canthus rostralis weak, no elevated intercanthal platform; 4) nostrils in protuberant fleshy swellings; 5) eye not protuberant; 6) tympanic apparatus indistinct; 7) reduced webbing between fingers I–II–III, but web between fingers III–IV extensive; 8) color of parietal pericardium unknown; 9) dorsum green with moderate yellow spots; 10) male call unknown.

In most features, except 4 and 6, *talamancae* resembles *C. fleischmanni* populations from southeastern Atlantic Costa Rica. It is possible that the apparent distinctiveness of the nostrils and tympanum are the result of desiccation in preservative. If *C. talamancae* is valid we have been unable to locate additional examples in our extensive series and surmise that study of living material is needed to clarify its status. Tentatively, we recognize it as a distinct form known only from the type locality.

NEW SPECIES FROM COSTA RICA

Among the materials collected in Costa Rica during our fieldwork that began in 1957, is a

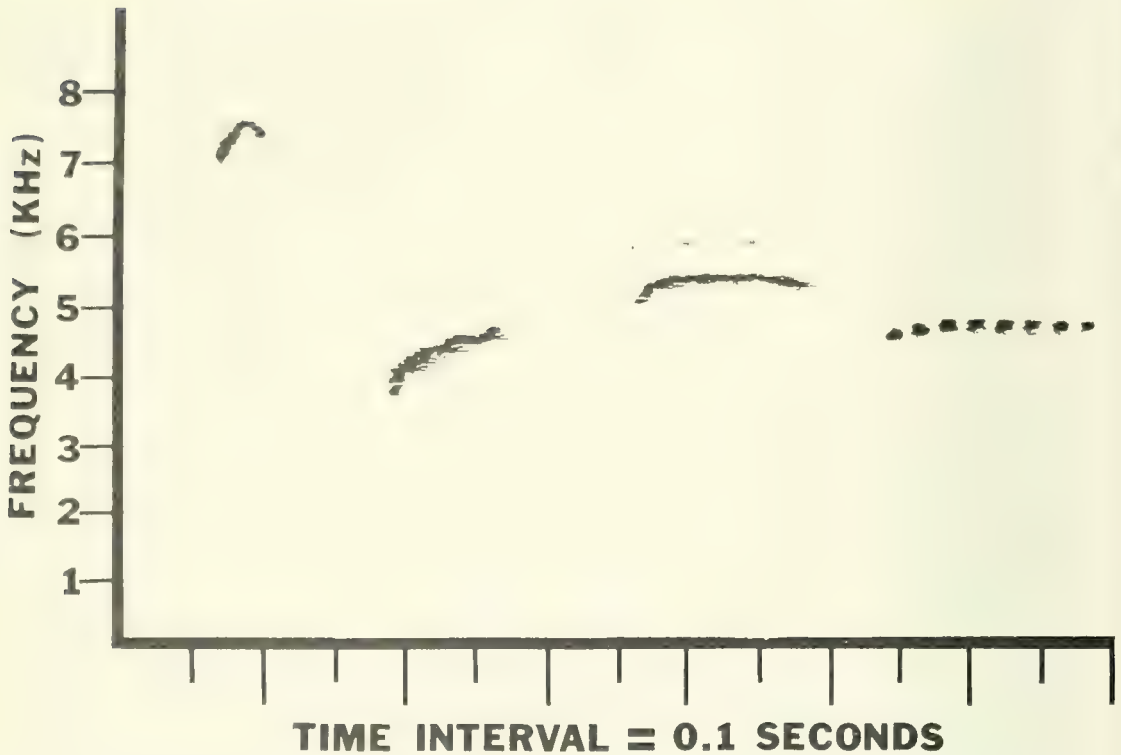


Figure 4. Sonograms of male vocalizations in glass-frogs of the *fleischmanni* group from Costa Rica. Left to right: *Centrolenella valerioi*, Provincia de Puntarenas: 3 km SW Rincon de Osa, November 22, 1968. *C. fleischmanni*, Provincia de San Jose: Curridabat, October 29, 1968; *C. vireovittata*, Provincia de San Jose: 0.5 km NE Alfombra, August 5, 1963; *C. colymbiophyllum*, Provincia de Puntarenas, 3 km W Rincon de Osa, August 22, 1969.

small series of striped *Centrolenella* of the *fleischmanni* group having a colorless pericardium. We first took this species in the Cordillera Costena between San Isidro de El General and the Pacific coastal village of Dominical in 1963. It occurs sympatrically with the reticulated species called *valerioi* in the present report, but because of Dunn's (1933) reference to a green stripe down the back in the type of the latter, we presumed that the striped form belong to Dunn's species. As pointed out above, the name *valerioi* is based on an example of the reticulated species and does not have a mid-dorsal stripe. The striped species cannot be referred to any other described form and may be known as:

Centrolenella vireovittata, new species

Holotype: LA 75141, (Fig. 5) an adult male, from Costa Rica: Provincia de San Jose: Canton Perez Zeledon: 0.5 km NE Alfombra: a place 16 km SW San Isidro de El General on the road to Dominical.

880 m; collected by Jay M. Savage and Norman J. Scott, July 17–18, 1963.

Diagnosis: The new species is immediately distinguished from all other centrolenids known from Mexico and Central America by its unique striped pattern (Fig. 5). No other striped species have been described in the family.

Definitive Characteristics: 1) head viewed from above, semicircular in outline with a truncate or slightly indented tip; 2) snout truncate in profile, loreal long; 3) canthus rostralis strong, with an elevated intercanthal platform; 4) nasal region markedly swollen and nostrils opening through elevated fleshy protuberances that lie on distinct raised ridges; 5) eyes not protuberant; 6) tympanic apparatus distinct; 7) reduced webbing between fingers I–II–III, but web between fingers III–IV, well-developed; 8) parietal pericardium colorless; 9) dorsum green with small to moderate yellow spots and a mid-dorsal green stripe bordered by a pair of paravertebral yellow stripes; 10) male call a rising whistled wheet.

Size: The holotype (22 mm) and five adult male paratypes (CRE 688, 2647, 6101–02, 7220A–B) range from 21.5–23 mm in standard length.

Remarks: Calling males of this species were taken at the type locality on three occasions, July 17–18 and August 5, 1963 and June 1, 1964. The frogs were found on the upper surfaces of leaves on low herbaceous bushes between 0.5–1 m above a shallow (5–7 cm deep) stream about 1.5 m wide. A sonograph of the call is shown (Fig. 4).

The type locality is in a Premontane Rain-forest, following the classification of Holdridge (1967), along the Pacific slope of the Cordillera Costena that separates the narrow coastal plain from the interior valley of the Rio General. This place, near the small village of Alfombra, is also the type locality for five other nominal taxa of reptiles and amphibians: *Anolis humilis marsupialis* Taylor, 1956; *Dermophis occidentalis* Taylor, 1955; *Dipsas tenuissima* Taylor, 1954; *Hyla legleri* Taylor, 1958; and *Neusticurus apodemus* Uzzell 1966. Although the *Anolis* and *Dermophis* are representatives of wide-ranging species (*A. humilis* and *D. parviceps*, respectively) the *Hyla* and *Dipsas* are valid species restricted in range to Pacific southwestern Costa Rica and adjacent extreme southwestern Panama. The *Neusticurus* and *Centrolenella* are not known to occur elsewhere.

At the type locality *Centrolenella vireovittata* was found sympatrically with *C. valerioi* of the *fleischmanni* group. *Centrolenella fleischmanni* and *C. colymbiophyllum* are known from a nearby locality Quebrada Salto, 6.4 km SW San Isidro de El General, near Palma on the road to Dominical, 750 m, on the interior slope of the Cordillera Costena. *Centrolenella granulosa* and *C. prosoblepon* of the *prosoblepon* group were also taken in virtual sympatry with *C. vireovittata* at the type locality.

DISTRIBUTIONS

Fleischmanni Group: The following lists include all Costa Rican locality records for the members of the *fleischmanni* group based upon material at the University of Southern California and the samples now at the University of Kansas that formed the basis for Taylor's (1958) review.

Centrolenella chirripoi—LIMON: Suretka on Rio Cocolis, 60 m (Fig. 6).

Centrolenella colymbiophyllum—ALAJUELA: Cariblanco; 1 km SW and Cinchona; CARTAGO: 8.8 km NE and Tapanti, Rio Quiri; GUANACASTE: Finca San Bosco; PUNTARENAS: Golfito; Las Cruces; 0.5 km SE, ESE, SW, 1.75 km ESE, 2.6 km ESE Monteverde; 3 km W, 3 km SW Rincon de Osa; SAN



Figure 5. Dorsal view of a male paratype (USC-CRE 6101) of *Centrolenella vireovittata*; scale equals 1 cm.

JOSE: Quebrada Salto, 6.4 km S San Isidro de El General; 6–1450 m (Fig. 6).

Centrolenella fleischmanni—ALAJUELA: Candelaria de Naranjo; Rio Cariblanco and Sarapiquí road; nr. Carrizal; Cinchona; nr. La Florencia; 3.2 km E La Fortuna; San Jose, nr. Rio Jesus; Sarchi; Rio Segundo; nr. Tacares; Tesalia; 8 km N Zarcero; CARTAGO: Cartago; 1.5 km SW Chitaria; Florencia; Instituto Interamericano de Ciencias Agricolas, nr. Turrialba; Moravia de Chirripo; 1 km S Orosi; 1 km E Pacayas; 1 km NE and Tapanti; 1–2 km SE Santa Teresa; GUANACASTE: 1.9, 3 km E, 2 km NW, 1.2 km SW Tilaran; HEREDIA: 1.6 km ENE La Uvita; San Jose de la Montana; LIMON: 16 km SW (Surayo), 20 km SW (Alto Lari) Amubri; Los Diamantes; Guacimo; Pandora; PUNTARENAS: 1.6 km SW Aguabuena; Rio Coton; 0.5 km ESE, 0.5 km SW Monteverde; SAN JOSE: Alto Guadalupe; Rio Claro-Rio La Hondura; Curridabat; Desamparados; 3.2 km WSW Escazu; El General; Guadalupe; Quebrada Salto, 6.4 km S and San Isidro de El General; San Jose; La Palma; Quizarra; San Pedro, Ciudad Universitaria; 50–1680 m (Fig. 7). This species is known from humid lowland and premontane forests from Mexico throughout Central America through Colombia to northwestern Ecuador and eastward through Venezuela to Surinam. It is possible that more than one species is involved in the material assigned to *fleischmanni* by Goin (1964), but only field studies give hope of clarifying their status.

Centrolenella talamancae—CARTAGO: Moravia de Chirripo, 1116 m (Fig. 6).

Centrolenella valerioi—ALAJUELA: Cariblanco, Rio Cariblanco and Sarapiquí rd.; CARTAGO: 1.5 km S Chitaria; Florencia; Moravia de Chirripo; nr. bridge over Rio Reventazon, 4.5 km SE Turrialba; LIMON: Suretka; PUNTARENAS: 6.4 km SE and Golfito; Palmar; 1 km W Platanillo; 3 km W, 2.5

km SW Rincon de Osa, Quebrada Aguabuena; 4.8, 5.1, 5.6 km NW Villa Neilly; SAN JOSE: 0.5 km NE Alfombra; Quizarra; La Palma. Also in PANAMA: COCLE: El Valle de Anton; 6–1500 m (Fig. 8).

Centrolenella vireovittata—SAN JOSE: 0.5 km NE Alfombra, 880 m (Fig. 6).

Sympatric occurrences of two or even three species of the *fleischmanni* group at one locality is not uncommon in Costa Rica. Sympatry is used in the sense that the individuals were collected at the same general locality at the same time of year. Detailed field studies will be required to demonstrate how various facets of the biology of these species may act to prevent interbreeding and to foster ecologic segregation at any particular site.

Centrolenella colymbiophyllum, *C. fleischmanni* and *C. valerioi* have all been taken at ALAJUELA: Cariblanco 830 m; *C. fleischmanni*, *C. talamancae*, and *C. valerioi* are sympatric at CARTAGO: Moravia de Chirripo, 1116 m. Localities where two species have been taken sympatrically are:

Centrolenella colymbiophyllum—*C. fleischmanni*: ALAJUELA: Cinchona, 1350 m; CARTAGO: Tapanti, 1200 m; PUNTARENAS: vicinity of Monteverde, 1400 m; SAN JOSE: Quebrada Salto, S San Isidro de El General, 750 m.

Centrolenella colymbiophyllum—*C. valerioi*—PUNTARENAS: Golfito 6 m; 3 km W Rincon de Osa, 25 m.

Centrolenella fleischmanni—*C. valerioi*—CARTAGO: Instituto Interamericano de Ciencias Agrícolas, 4–5 km SSE Turrialba, 602 m; SAN JOSE: La Palma, 1500 m; Quizarra, 720 m.

Centrolenella valerioi—*C. vireovittata*—SAN JOSE: 0.5 km NE Alfombra, 880 m.

Centrolenella valerioi and *C. chirripoi* are almost certainly sympatric at LIMON: Suretka, 60 m.

Prosoblepon and *Pulverata* Groups—In earlier papers (Starrett, 1960, Savage, 1967; Savage and Starrett, 1967) we have discussed the distinguishing characteristics and general distribution of members of these groups in Costa Rica and Panama. We take this opportunity to provide a full listing of Costa Rican localities in order that our views on the current systematic status and distributions for Costa Rican glass-frogs may be available in a single paper.

Prosoblepon Group

Centrolenella albomaculata—ALAJUELA: Sarchi; Tesalia; CARTAGO: 1.5 km S Chitaria; nr. Turrialba; GUANACASTE: 2 km NW, 1.2 km SW and Tilaran; LIMON: 20 km SW Amubre (Alta Lari); 1.6 km E, 1.6 km N and Los Diamantes; PUNTARENAS: 6 km SE Golfito; Finca Loma Linda, 3.2 km SSW Canas Gordas; Rio Ferruviosa 6 km S Rincon de Osa; SAN JOSE: nr. Juntas de Rio General; Quebrada Salto, 6.4 km S and San Isidro de El General; 4–1180 m. Also known from PANAMA: COCLE: El Valle de Anton (Fig. 9).

Centrolenella euknemos—SAN JOSE: 1.5 km S Alto La Palma; Rio Claro—Rio La Hondura; 1150–1500 m. Also known from PANAMA: CANAL ZONE: Summit; DARIEN: Rio Jaque 1.5 km above Rio Imamado; Laguna; PANAMA: S slope Cerro Campana; SAN BLAS: Summit Camp (Fig. 10).

Centrolenella granulosa—ALAJUELA: nr. Concepcion; La Garita; Tesalia; CARTAGO: 1.5 km SW Chotaria; Moravia de Chirripo; 5 km SE Turrialba; GUANACASTE: 3 km NW Arenal; LIMON: Los Diamantes; PUNTARENAS: 4.8 km, 5.1 km NW Villa Neilly; 3 km W Rincon de Osa; SAN JOSE: 0.5 km NE Alfombra; Quebrada Salto, 6.4 km S San Isidro de El General; 25–1116 m.

Also known from PANAMA: BOCAS DEL TORO: 4.8 km W Almirante; CHIRIQUI: Progreso; DARIEN: Reversa de Pava, Rio Tuira; PANAMA: nr. Rio Chico Hydrographic Station. Villa (1972) tentatively identified specimens from Nicaragua as this form. We have seen examples (KU 85474) from NICARAGUA: MATAGALPA: Finca Tepeyac to confirm Villa's records from the same departamento at La Cumplida and San Jose de la Montana (Fig. 10).

Centrolenella ilex—ALAJUELA: nr. Concepcion; 8 km NW Ciudad Quesada; CARTAGO: 1.5 km SW Chitaria; LIMON: 16 km SW Amubre (Surayo); 250–775 m; PANAMA: no other data, FM 153710, first record for the republic (Fig. 9).

Centrolenella prosoblepon—ALAJUELA: 0.3 km N Salto Angel; Cariblanco; nr. Carrizal; 1 km S and Chichona; La Fortuna; San Jose, nr. Rio Jesus; 4.8 km S Ciudad Quesada; Sarchi; 1.6 km, 8 km S Zarcero; CARTAGO: Cartago; Casa Mata; 1.5 km S Chitaria; Santa Cruz; Moravia de Chirripo; Pacayas; Tapanti, Rio Quiri; Santa Teresa; 3.2 km SE Tres Rios; HEREDIA: 4.3 km S Santa Domingo de El Roble; 1.6 km NW La Uvita; LIMON: 8 km SW Amubre; Los Diamantes; La Junta; Puerto Limon; PUNTARENAS: Aguabuena; Las Cruces; El Helechales; 0.5 km SE, 0.5 km SW Monteverde; 1 km W Platanillo; 5 km SSW Rincon de Osa, Rio Ferruviosa; SAN JOSE: 0.5 km NE Alfombra; Santa Ana, Rio Oro; Bebedero de Escazu; Rio Claro—Rio La Hondura; 1 km S San Cristobal Sur; 3.2 km WSW Escazu; San Isidro de Coronado; La Palma; Quebrada Salto, 6.4 km S San Isidro de El General; San Pedro; Ciudad Universitaria; Salitral; 20–1900 m (Fig. 11). The species is also known from southeastern Atlantic lowland Nicaragua and in humid situations on both coasts of western and central Panama south to northwestern Ecuador.

Centrolenella spinosa—ALAJUELA: 3.2 km E La Fortuna; Tesalia; HEREDIA: La Selva; LIMON: Bambu; Los Diamantes; PUNTARENAS: 2.5 km SW Rincon de Osa; 20–260 m. Also known from PANAMA: CANAL ZONE: Barro Colorado Island (Fig. 10). We also have seen specimens probably representing this species from western Colombia and Ecuador.



Figure 6. Distribution of Costa Rican glass-frogs allied to *Centrolenella fleischmanni*; the dotted line indicates the 1500 m contour.



Figure 7. Distribution of *Centrolenella fleischmanni* in Costa Rica; the dotted line indicates the 1500 m contour.



Figure 8. Distribution of *Centrolenella valerioi* in Costa Rica; the dotted line indicates the 1500 m contour.



Figure 9. Distribution of Costa Rican glass-frogs of the *prosoblepon* group; the dotted line indicates the 1500 m contour.



Figure 10. Distribution of Costa Rican frogs of the *prosoblepon* group; the dotted line indicates the 1500 m contour.



Figure 11. Distribution of *Centrolenella prosoblepon* in Costa Rica; the dotted line indicates the 1500 m contour.



Figure 12. Distribution of *Centrolenella pulverata* in Costa Rica; the dotted line indicates the 1500 m contour.

Pulverata Group

Centrolenella pulverata—ALAJUELA: Rio Ron Ron, 8 km N Ciudad Quesada; Tesalia; CARTAGO: Florencia; LIMON: 14.5 km SW Amubre; 1.6 km E and Los Diamantes; PUNTARENAS: 2.5 km SW, 3 km W Rincon de Osa; SAN JOSE: nr. Juntas de Rio General; Quebrada Salto, 6.4 km S San Isidro de El General. Also known from PANAMA: CHIRIQUI: Progreso; DARIEN: Rio Jaque, 1.5 km above Rio Imamado; Rio Siluganti. Villa (1972) tentatively included this species in the fauna of Nicaragua without further data. He apparently had seen a specimen (KU 85476) from NICARAGUA: MATAGALPA: Finca Tepeyac, which is unquestionably *pulverata* (Fig. 12).

Sympatric occurrences of two to four species of the *prosoblepon* group at a single locality, often together with *C. pulverata* are common in Costa Rica. Although all species have not been taken at precisely the same locality, or on the same date, four species of the *prosoblepon* group (*albomaculata*, *granulosa*, *prosoblepon*, and *spinosa*) and *pulverata* occur together in the area immediately southwest of Rincon de Osa, Provincia de Puntarenas (20–30 m) on the Pacific lowlands, although *albomaculata* has not actually been taken in the same stream course with the others. All five of these forms occur in the same stream, at Los Diamantes, Provincia de Limon (260

m) on the Atlantic versant. Two species of the *fleischmanni* group (*colymbiphyllum* and *valerioi*) occur at the former locality making a total of seven sympatric glass-frogs at that place and one (*fleischmanni*) at Los Diamantes for a total of six species. Other areas with high species numbers include: the Rio Lari canyon southwest of Amubre, Provincia de Limon (300–800 m), with *C. albomaculata*, *C. ilex*, *C. prosoblepon*, and *C. pulverata* and the type species of the *fleischmanni* group; the area just southwest of Turrialba, Provincia de Cartago (600 m) with *C. albomaculata*, *C. granulosa*, and *C. pulverata* and *C. fleischmanni*, and *C. valerioi* of the *fleischmanni* group; the region where the Rio Chitaria crosses the Turrialba to Puerto Limon road, 1.5 km S Chitaria, where *C. albomaculata*, *C. granulosa*, *C. ilex*, and *C. prosoblepon* occur with *C. valerioi* of the *fleischmanni* group; at Tesalia, Provincia de Alajuela (600 m) where *C. albomaculata*, *C. granulosa*, *C. spinosa*, and *C. pulverata* occur with *C. fleischmanni* and Quebrada Salto, Provincia de San Jose (750 m) where *C. albomaculata*, *C. granulosa*, and *C. pulverata* are found with *C. colymbiphyllum* and *C. fleischmanni*. Additional records of sympatry within the *prosoblepon* and *pulverata* groups include:

albomaculata—*granulosa*—PANAMA: COCLE: El Valle de Anton, 800 m.

albomaculata—*pulverata*—SAN JOSE: nr. Juntas de Rio General, 530 m.

albomaculata—*prosoblepon*—ALAJUELA: Sarchi, 970 m.

euknemos—*prosoblepon*—SAN JOSE: 1.5 km S Alto La Palma, 1500 m; Río Claro—Río La Hondura, 1500 m.

euknemos—*pulverata*—PANAMA: DARIEN: Río Jaque 1.5 km above Río Imamado, 50 m.

granulosa—*ilex*—ALAJUELA: nr. Concepción, 547 m.

granulosa—*prosoblepon*—CARTAGO: Moravia de Chirripo, 1116 m; SAN JOSE: 0.5 km NE Alfombra; 880 m.

granulosa—*pulverata*—PANAMA: CHIRIQUI Progreso, 23 m.

ilex—*pulverata*—ALAJUELA: 8 km N Ciudad Quesada, 250 m.

The species of the *prosoblepon* and *pulverata* groups usually occur sympatrically with one to as many as three species of the *fleischmanni* group at most localities. The accompanying table (Table 1) summarizes the sympatric occurrences of all Costa Rican species of glass-frogs.

DISTRIBUTIONAL PATTERNS

Geographic Patterns: The geographic distribution of Costa Rican centrolenids is summarized below (Table 2) in a fashion comparable to that employed by Savage and Heyer (1969) for tree-frogs of the family Hylidae. Five major geographic regions are recognized for this purpose:

A. Atlantic Lowlands—entire Caribbean Coastal Plain

B. Northwest Pacific Lowlands—region from level of the mouth of the Golfo de Nicoya northwestwards

C. Southwest Pacific Lowlands—region southeast of the Golfo de Nicoya

D. Cordilleras Central—Tilarán—mountains of the Cordillera Central and its northwestern extensions

E. Cordillera de Talamanca—mountains of southern Costa Rica

The Costa Rican forms may be grouped as indicated below. No species are found in the dry seasonal forest areas of Pacific northwest Costa Rica.

1. Wide-ranging forms—found on both Atlantic and Pacific lowlands and sometimes onto mountain slopes (9).

a. Restricted to lowlands and lower slopes (5): *pulverata*; *albomaculata*; *granulosa*; *ilex*; *spinosa*.

b. Absent from Talamancas (1): *colymbiphyllum*.

c. Ubiquitous (3); *fleischmanni*; *valerioi*; *prosoblepon*.

2. Atlantic lowland form (1): *chirripoi*.

3. Southwest Pacific slope form (1): *vireovittata*.

4. Cordilleran forms (2).

a. Cordillera Central (1): *euknemos*.

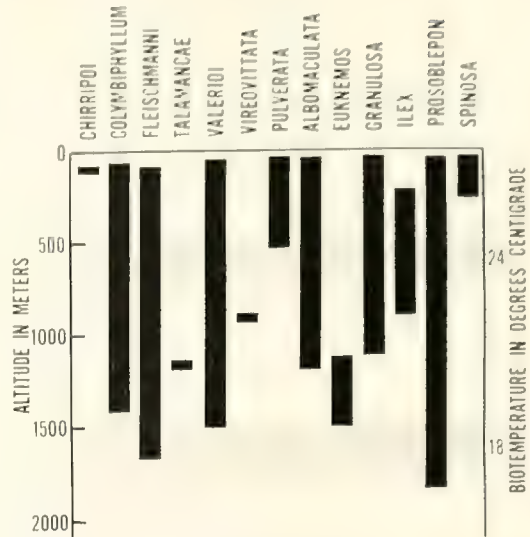


Figure 13. Altitudinal distribution of Costa Rican glass-frogs. See text for explanation.

b. Atlantic slope of Cordillera de Talamanca (1): *talamancae*.

Ecologic Patterns: The altitudinal distribution of Costa Rican centrolenids is summarized (Fig. 13). All species seem to be restricted to the Tropical Lowland and Premontane temperature related altitudinal zones of Holdridge (1967), except for the wide-ranging species *C. fleischmanni* and *C. prosoblepon* which may reach the extreme lower margins of the lower Montane zone. Most of the other species are found in both Tropical Lowland and Premontane zones, but *C. chirripoi*, *C. pulverata*, and *C. spinosa* are restricted to lowland localities and *C. talamancae*. *C. vireovittata*, and *C. euknemos* are recorded only from Premontane sites.

Relatively little is known regarding the ecologic requirements of the glass-frogs. The mosaic pattern of their distributions where many species occur sympatrically at different sites but always in different species combinations, makes interpretation of patterns impossible. Some field observations suggest that the height and density of vegetation along the streams, where breeding takes place, may regulate species composition.

Centrolenella fleischmanni and *C. prosoblepon*, for example, occur most commonly along streams with an opening in the canopy above them or where heavy low (1–2 m high) herbaceous vegetation occurs along the stream. *Centrolenella colymbiphyllum*, *C. pulverata*, *C. albomaculata*, *C. euknemos*, *C. granulosa*, and *C. spinosa* are rarely found along streams that lack heavy over-

TABLE 1. Sympatric occurrences of Costa Rican centrolenids.

	<i>chrysolaema</i>	<i>fulvicauda</i>	<i>fleischmanni</i>	<i>talamaneae</i>	<i>valerioi</i>	<i>vireovittata</i>	<i>albomaculata</i>	<i>euknemios</i>	<i>granulosa</i>	<i>ilex</i>	<i>prosohlepon</i>	<i>spinosa</i>
<i>chrysolaema</i>												
<i>fulvicauda</i>												
<i>fleischmanni</i>		X										
<i>talamaneae</i>			X									
<i>valerioi</i>		X	X	X								
<i>vireovittata</i>					X							
<i>albomaculata</i>		X	X		X							
<i>euknemios</i>			X		X							
<i>granulosa</i>		X	X	X	X	X	X					
<i>ilex</i>			X		X		X		X			
<i>prosohlepon</i>		X	X		X	X		X	X	X		
<i>spinosa</i>		X	X		X		X		X		X	
<i>pulverata</i>		X	X		X		X		X	X	X	X

hanging forest stands. *Centrolenella valerioi*, *C. vireovittata*, and *C. ilex* tend to occur along fast-moving trickles, seeps, or small waterfalls almost completely covered by low shrubs. Some vertical stratification of calling males at sites such as Rincon de Osa (Pacific) and Los Diamantes (Atlantic) where six or seven species of *Centrolenella* occur sympatrically is suggested by our field notes. Presumably maximum numbers of species are found at localities with a mixture of ecologic conditions and the mosaic pattern of geographic distribution and sympatric occurrence relate to the presence or absence of the several habitats at a particular site. Intensive fieldwork on ecologic partitioning by glass-frogs of the habitat at such localities may provide deeper insight into the nature of ecologic niches and species diversity in tropical lowland communities.

RELATIONSHIPS WITHIN THE FLEISCHMANNI GROUP

We (Savage, 1967; Savage and Starrett, 1967) have previously discussed the characterization of the *prosohlepon* and *pulverata* groups of the genus *Centrolenella* and the probable relations among Central American species placed in these groups. Centrolenids as a rule show a mosaic of primitive and advanced characteristics that make any attempt to establish relationships difficult. A review of the 10 characters used to diagnose the six Costa Rican species of the *fleischmanni* group reaffirms the difficulties. Of these 10 features, four related to head form and proportions, the condition of the tympanum, the color of the pericardial peritoneum, some aspects of the basic color pattern and the structure of the male call suggest relations between species. The

TABLE 2. Geographic Distribution of Costa Rican centrolenids.

	A	B	C	D	E
CHIRRIPOI	†				
COLYMBIPHYLLUM	X		X	X	
FLEISCHMANNI	X		X	X	X
TALAMANCAE					†
VALERIOI	X		X	X	
VIREOVITTATA			†		
PULVERATA	X		X		
ALBOMACULATA	X		X		
EUKNEMOS				X	
GRANULOSA	X		X		
ILEX	X		X		
PROSOBLEPON	X		X	X	X
SPINOSA	X		X		
TOTALS	10	0	10	5	3

† Single Record.

following unique characters segregate out unique species: truncate snout and protuberant eyes are found only in *colymbiphyllum*; extensive webbing between fingers II–III only in *chirripoi*; concealed tympanum only in *fleischmanni*; mid-dorsal and paravertebral stripes only in *vireovittata*; and dark reticulated pattern only in *valerioi*.

Among known centrolenids, the *fleischmanni* group appears to be most closely related to the monotypic *pulverata* group. This latter lineage shares a mosaic of distinctive features, some in common with the *fleischmanni* group and others with the *prosoblepon* group, and probably is similar to the ancestral stock that gave rise to the two lines. *Centrolenella pulverata* agrees with the *fleischmanni* group in basic integumentary pigmentation, in the bulb-shaped liver, in having white pigment in the visceral peritoneum, a colorless parietal peritoneum and green eggs. In addition, the species agrees with some members of the latter group in having a white parietal pericardium and extensive webbing between fingers II–III. It seems likely that the *fleischmanni* group arose from an ancestor that was a precursor to, and resembled *C. pulverata* in these features.

Within the *fleischmanni* group, *C. chirripoi* most closely approaches the *pulverata* group and the proposed ancestral stock in the above mentioned features, but particularly in having extensive webbing between fingers II–III. *Centrolenella chirripoi*, *C. talamancae*, and *C. fleischmanni* seem to form a subgroup within the

fleischmanni line characterized by having a rounded head outline, a weak canthus rostralis and by lacking a well-developed intercanthal platform. The principal differences distinguishing among the three species are the reduced webbing between fingers II–III in *talamancae* and *fleischmanni* as opposed to the extensive webbing of *chirripoi*; the distinct tympanum in *chirripoi*, indistinct tympanum in *talamancae* and concealed tympanum in *fleischmanni*; and the somewhat swollen nostrils in *chirripoi* and *talamancae* as opposed to the nostrils not swollen in *fleischmanni*. On the basis of these features, *chirripoi* appears to be the most primitive species and *fleischmanni* the most advanced. *Centrolenella talamancae* is intermediate but is most closely allied to the advanced species.

A second subgroup consisting of *vireovittata*, *valerioi*, and *colymbiphyllum* is characterized by having a semi-circular or truncate head outline with a strong indentation between the nostrils, a strong canthus rostralis, and a strongly developed intercanthal platform. All members of this subgroup have a distinct tympanum and strongly swollen nostrils.

Other characteristics tend to vary between the two sub-groups recognized on the basis of basic head form and structure. *Centrolenella fleischmanni* and *valerioi* have a white parietal pericardium while *colymbiphyllum* and *vireovittata* have the pericardium colorless (Fig. 2). Presumably the other members of the *fleischmanni* group have white pigment covering the heart. *Centrolenella fleischmanni* and *vireovittata* share similar male vocalizations while those of *valerioi* and *colymbiphyllum* (Fig. 4) are each distinctive. The basic color pattern for most species is comprised of whitish to yellow spots on a green background (Fig. 3A–B), but the reticulated pattern of *valerioi* (Fig. 3D) and the striped pattern of *vireovittata* (Fig. 5) are distinctive. The pattern of the latter clearly seems derived from the basic coloration found elsewhere in the group by fusion of a number of yellow spots in the paravertebral regions to form a regular pair of longitudinal yellow stripes, separated on the mid-line by a green vertebral stripe. Elsewhere on the body the pattern is identical to the other species, exclusive of *valerioi*.

Within the subgroup comprised of *colymbiphyllum*, *valerioi*, and *vireovittata*, each species is trenchantly distinct and not obviously closely allied to any other. *Centrolenella colymbiphyllum*

retains the basic color pattern of whitish to yellow spots on a green background but in other respects: head shape, protuberant eyes, colorless pericardium and the distinctive male call, seems the most advanced Costa Rican species. *Centrolenella vireovittata* also has a colorless pericardium but has a unique striped pattern. In general head morphology and male call, this species approaches the *fleischmanni* subgroup more closely than *colymbiophyllum* or *valerioi*. The latter species is morphologically close to *vireovittata* but has a white pericardium. It further differs from that species and all other Central American forms in its unique reticulated pattern and distinctive male call. *Centrolenella valerioi* occurs sympatrically with *vireovittata*, *fleischmanni*, and *colymbiophyllum*. The call of *colymbiophyllum* is distinct and this species occurs with *valerioi* and *fleischmanni*. The two species with the most similar calls, *fleischmanni* and *vireovittata* apparently do not occur together suggesting that call displacement may be involved in the speciation of these frogs. These data indicate the origin of the second subgroup from an ancestral stock not unlike *C. chirripoi*, with a white pericardium and a male call similar to that of *fleischmanni*, through a reduction of the webbing between fingers II–III and modifications in head form and structure. Within the subgroup each species shows a peculiar combination of characteristics that suggests independent origin from a common ancestral stock. Although the three species may be arranged along a primitive to advanced scale from *vireovittata* through *valerioi* to *colymbiophyllum*, each form is so distinctive as to preclude derivation of any of them from any others or from a progenitor closely resembling any known living species.

A KEY TO THE GLASS-FROGS, GENUS *CENTROLENELLA*, IN COSTA RICA

1. a. Vomerine teeth present; bones green in life 2
b. No vomerine teeth; bones white in life 8
2. a. Snout vertical to rounded in profile 3
b. Snout strongly obtuse in profile 6
3. a. Dorsum uniform or with a few large light or dark spots or heavily spotted with dark; no fleshy ridge along posterior margin of lower arm 4
b. Dorsum marked with numerous light spots; distinct fleshy ridge along posterior margin of lower arm *C. albomaculata*.
4. a. No free prepollex or prepollical spine; dorsum smooth; adult males to 27 mm, females to 32 mm 5
b. A free prepollex or prepollical spine; dorsum weakly granular; adult males to 20 mm, females to 23 mm *C. spinosa*.
5. a. Webs between toes III–IV–V not reaching ultimate subarticular tubercle on toes III and V, not reaching penultimate subarticular tubercle on toe IV; a humeral hook present in adult males and some females; snout sub-ovoid in dorsal outline; nostrils not elevated on protuberant ridges; dorsal color uniform or with numerous small dark spots *C. prosoblepon*.
b. Webs between toes III–IV–V reaching ultimate subarticular tubercle on toes III and V, reaching penultimate subarticular tubercle on toe IV; no humeral hook; snout semicircular in dorsal outline; nostrils elevated on protuberant ridges; dorsum uniform or with a few large light spots, never marked with numerous dark spots *C. ilex*.
6. a. A distinct fleshy fringe along posterior margin of lower arm and lower leg; dorsal coloration with distinct light spots 7
b. No fleshy fringe along arms or legs; dorsum uniform or with a few large black spots *C. granulosa*.
7. a. A white peritoneal sheath obscures most of visceral organs, in life; colorless hepatic peritoneum; interorbital broad, width exceeding orbital diameter; snout elongate, distance from eye to tip of snout greatly exceeding orbital diameter; web between fingers II–III not nearly as extensive as between fingers III–IV, restricted to base of fingers *C. euknemos*.
b. Parietal peritoneum colorless so that viscera visible in life; hepatic and other visceral peritoneum white; interorbital narrow, less than orbital diameter; snout short, distance from eye to tip of snout equal to orbital diameter; web between fingers II–III almost as extensive as between fingers III–IV *C. pulverata*.
8. a. Web between fingers II–III not nearly as extensive as between fingers III–IV, restricted to base of fingers 9
b. Web between fingers II–III almost as extensive as between fingers III–IV *C. chirripoi*.
9. a. Dorsum without a distinct straight mid-dorsal green stripe bordered on either side by yellow stripes; color green with small yellow spots or reticulated with green and yellow, in life, uniform white to yellow or with a dark reticulum in preservative 10
b. Dorsum with a distinct straight mid-dorsal green stripe bordered on either side by yellow stripes, in life; dark stripe clearly indicated by purplish to brownish pigment in preservative; pericardium colorless *C. vireovittata*.

10. a. Dorsal pattern of small to moderate yellow spots on a green background in life; almost uniform yellowish to whitish although often with small minute punctations of brown or purple in preservative..... 11
 b. Dorsal pattern in life a broad reticulum of green with black punctations and yellow; black punctations clearly demarcate reticulum in preservative; pericardium white in life *C. valerioi*.
11. a. Nostrils in strongly protuberant fleshy swellings; tympanic apparatus distinct..... 12
 b. Nostrils open through very slightly indicated fleshy swellings; tympanic apparatus concealed; pericardium white in life *C. fleischmanni*.
12. a. Head viewed from above rounded, with a weakly pointed snout; canthus rostralis weak, no elevated intercanthal platform; eyes not protuberant *C. talamancae*.
 b. Head viewed from above truncate with an indentation between nostrils; canthus rostralis strong, with an elevated intercanthal platform; eyes protruding laterally well beyond level of lip margin; pericardium colorless *C. colymbiophyllum*.

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THE CHIGGERS (ACARINA, TROMBICULIDAE) PARASITIZING THE SIDEBLOTCHED LIZARD (*UTA STANSBURIANA*) AND OTHER LIZARDS IN JOSHUA TREE NATIONAL MONUMENT, CALIFORNIA

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ABSTRACT: Chiggers were found on *Uta stansburiana* and on ten other lizard species. A total of 923 (39 percent) of the 2354 examined lizards possessed chiggers. The abundance and seasonal occurrence of the chiggers were determined in a study plot and in the three plant belts of the Monument. Temperature and precipitation influenced the emergence and disappearance of larvae on the hosts. Four chiggers were present during warm weather; and one species was present on hosts in the cool weather.

In 1960, studies of the flora and fauna of Joshua Tree National Monument were initiated. Special attention was directed to the ectoparasites of vertebrates. Within the Monument, approximately 55 species of chiggers have been obtained from more than 4600 vertebrates sampled. Larval chiggers have been found on 53 species of terrestrial vertebrates: two frogs, 13 lizards, 7 snakes, 3 birds, and 28 kinds of mammals. This report deals with the chiggers found on *Uta stansburiana* and other lizards.

The Monument contains more than 787 square miles (2039 sq km) ranging in elevation from 1000 to 5600 feet (305-1708 m). The mountains and high plateaus decrease in elevation from the northwest to southeast, and are surrounded by lower valleys and basins. The entire Monument is classified as desert, although certain high areas have scattered patches of coastal chaparral. It is divided into the following three plant belts as defined and mapped by Miller and Stebbins (1964).

1. The Creosote Bush plant belt (48 percent of the Monument) occurs in the low desert valleys from

1000 (305 m) to approximately 3000 feet (1015 m). It is characterized by Creosote Bushes (*Larrea divaricata*) and other shrubs and cacti in addition to scattered trees along the southern border. This is the hottest and usually the driest part of the Monument. The substrate is frequently sandy, gravelly or desert pavement. Except for a few oases, there is no permanent surface water.

2. The Yucca plant belt (34 percent) ranges from 3000 feet (1015 m) to and occasionally above 4200 feet (1280 m). It contains many rocky areas and plateaus and is covered by grasses, numerous shrubs, yuccas (*Yucca schidigera*), Joshua trees (*Yucca brevifolia*), and junipers.

3. The Pinyon plant belt (18 percent) usually occurs above 4200 feet (1280 m) up to 5600 feet (1708 m) in the mountains and contains scattered pinyons, oaks, junipers, and Joshua trees. Grasses and many kinds of shrubs form a ground cover which is well developed in alluvial fans. The rainfall usually is greatest in this plant belt. As in the other belts, there is virtually no surface water.

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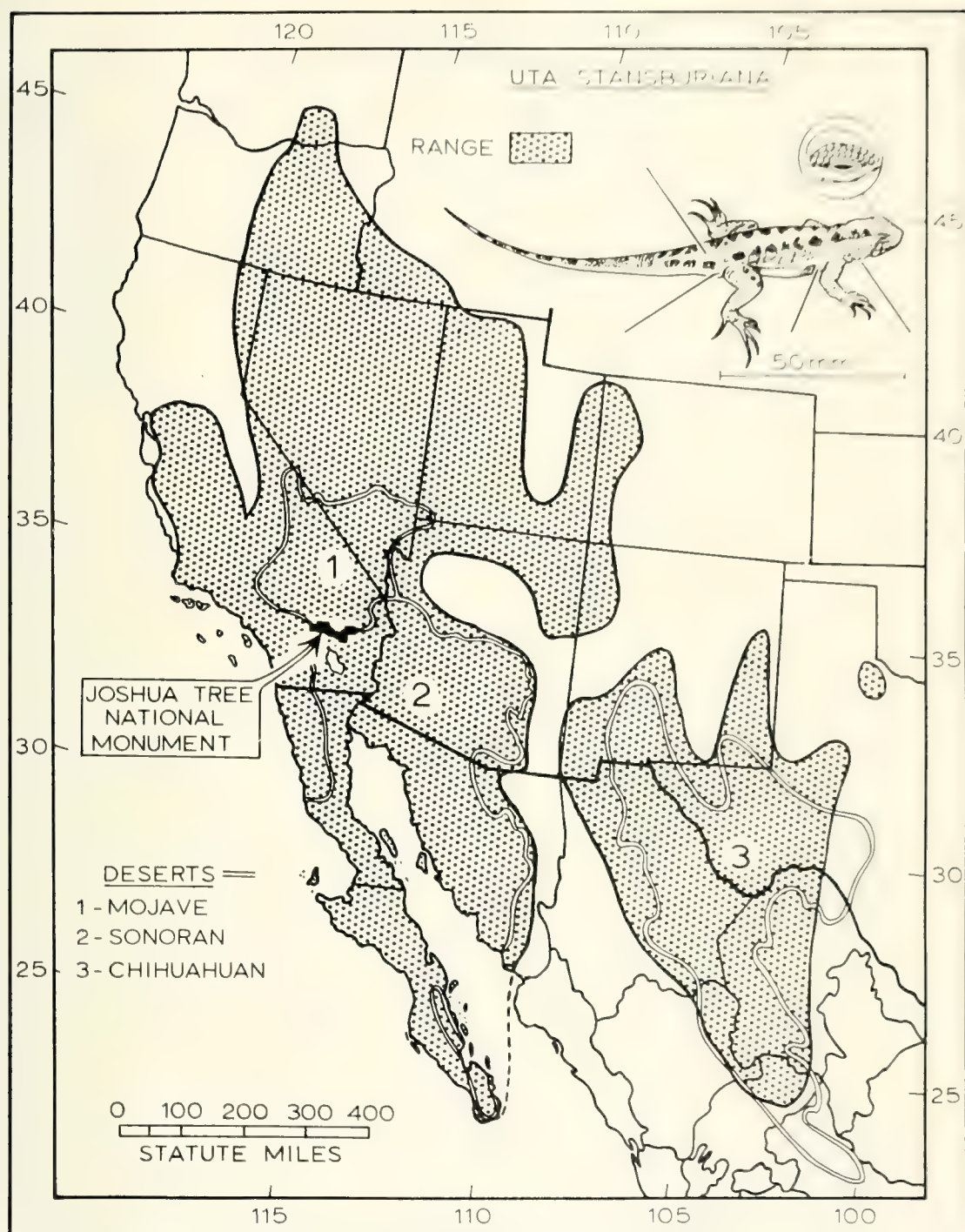


Figure 1. The Side-blotched Lizard, *Uta stansburiana*, and its geographic distribution. The sites of chigger attachment are denoted by solid lines (front to rear): 1) upper eyelid, with insert showing attached larvae of *Neotrombicula harperi*; 2) lateral nuchal fold; 3) axilla; 4) groin; and 5) base of tail. The three major deserts and Joshua Tree National Monument are delineated. The distribution is based on Tinkle (1967), McKinney (1971), and others.

TABLE 1. The lizards from Joshua Tree National Monument examined for chiggers (1959–1966), and found to have the same species of chiggers as *Uta stansburiana*. The number below the line represents the total examined, above is the number of lizards with chiggers.

Species of lizard	Jan. Nov.										
	Total	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Dec.
<i>Uta stansburiana</i>	<u>744</u> 1703	<u>79</u> 93	<u>103</u> 141	<u>124</u> 282	<u>37</u> 107	<u>48</u> 72	<u>21</u> 129	<u>54</u> 239	<u>88</u> 193	<u>133</u> 288	<u>57</u> 159
<i>Sceloporus occidentalis</i>	<u>67</u> 233	<u>0</u>	<u>18</u> 23	<u>10</u> 45	<u>4</u> 26	<u>11</u> 30	<u>5</u> 17	<u>6</u> 30	<u>9</u> 34	<u>1</u> 20	<u>3</u> 8
<i>Cnemidophorus tigris</i>	<u>24</u> 122	<u>0</u>	<u>0</u> 9	<u>3</u> 23	<u>11</u> 41	<u>2</u> 16	<u>3</u> 9	<u>2</u> 8	<u>0</u> 3	<u>3</u> 13	<u>0</u>
<i>Callisaurus draconoides</i>	<u>18</u> 80	<u>0</u>	<u>0</u> 5	<u>3</u> 20	<u>2</u> 21	<u>3</u> 5	<u>0</u> 4	<u>8</u> 14	<u>0</u>	<u>2</u> 10	<u>0</u> 1
<i>Sceloporus magister</i>	<u>19</u> 55	<u>0</u>	<u>0</u> 2	<u>0</u> 9	<u>9</u> 13	<u>2</u> 8	<u>5</u> 11	<u>3</u> 6	<u>0</u>	<u>0</u> 2	<u>0</u>
<i>Dipsosaurus dorsalis</i>	<u>11</u> 39	<u>0</u>	<u>1</u> 2	<u>0</u> 5	<u>1</u> 18	<u>1</u> 2	<u>7</u> 8	<u>1</u> 1	<u>0</u> 1	<u>0</u> 2	<u>0</u>
<i>Phrynosoma coronatum</i>	<u>5</u> 37	<u>0</u>	<u>0</u> 1	<u>0</u> 8	<u>1</u> 20	<u>0</u>	<u>1</u> 3	<u>0</u>	<u>2</u> 4	<u>1</u> 1	<u>0</u>
<i>Phrynosoma platyrhinos</i>	<u>12</u> 27	<u>0</u>	<u>0</u>	<u>1</u> 2	<u>7</u> 9	<u>2</u> 7	<u>2</u> 6	<u>0</u> 3	<u>0</u>	<u>0</u>	<u>0</u>
<i>Crotaphytus wislizeni</i>	<u>12</u> 25	<u>0</u>	<u>0</u>	<u>0</u> 1	<u>4</u> 8	<u>2</u> 4	<u>2</u> 2	<u>3</u> 4	<u>1</u> 4	<u>0</u> 2	<u>0</u>
<i>Crotaphytus collaris</i>	<u>9</u> 13	<u>0</u>	<u>2</u> 2	<u>0</u> 2	<u>2</u> 2	<u>2</u> 3	<u>0</u>	<u>2</u> 3	<u>1</u> 1	<u>0</u>	<u>0</u>
<i>Urosaurus graciosus</i>	<u>2</u> 15	<u>0</u>	<u>0</u> 1	<u>0</u> 1	<u>1</u> 7	<u>0</u>	<u>1</u> 1	<u>0</u> 2	<u>0</u>	<u>0</u> 3	<u>0</u>
Total with chiggers	<u>923</u>	<u>79</u>	<u>124</u>	<u>141</u>	<u>79</u>	<u>73</u>	<u>47</u>	<u>79</u>	<u>101</u>	<u>140</u>	<u>60</u>
Total lizards examined	2354	93	186	398	272	147	190	314	240	346	168
Percent with chiggers	39	85	67	35	29	50	25	25	42	44	36

DISCUSSION

The most abundant and widespread vertebrate in the Monument is the diurnal Side-blotched Lizard, *Uta stansburiana* (Baird and Girard); a small insectivorous iguanid lizard which occurs throughout western North America (Fig. 1). The adults measure 48–55 mm (1.75–2.25 inches) snout-vent, and the complete tail is 1.25 to 1.5 times longer than the head and body. The hatchlings measure 21–22 mm snout-vent and juveniles are 25–30 mm within two months after hatching. Adult size is reached in one full

year, and individuals rarely live longer than two full years. Usually mating is in the spring and most eggs are laid in late spring and hatch in the summer (July–August). In August and September, most of the individuals are juveniles.

Each lizard sheds its skin several times each year, and probably a few partially engorged chiggers are cast off with the dead skin. Larvae seem to attach more readily to new skin than to old, and rarely attach at previous feeding sites which have not been repaired.

Uta stansburiana is active throughout the year,

and from November through February it is virtually the only active lizard (Table 1). The greatest activity of adults seems to be in the spring (March and April). Its small size allows rapid warming in brief warm spells and, being a ground-dwelling lizard, it usually basks on rocks, fallen tree limbs or open soil, rarely climbing trees or shrubs. It regularly seeks shelter in rodent burrows, rock crevices, and beneath rocks and plant debris. They are most numerous above 3000 feet (1000 m) in the Yucca and Pinyon plant belts, although they are common in every habitat except in those low areas with shifting sand.

Territoriality is exhibited by the males and fifty square feet (4.65 sq m) would circumscribe an average male territory. The females seem to lack territoriality, but they do not move extensively. Two adult Side-blotched Lizards (one male and one female) per fifty square feet in suitable habitats would seem to be a reasonable estimate of the average population density for the spring and early summer months. Samples covering four years of a population in an acre plot in the Pinyon plant belt (16 squares, each of approximately fifty square feet) revealed an average of 36 adults and subadults, slightly over the 32 estimate. However, in three of four years, the average was only 21 lizards. Inasmuch as this was the average of lizards captured in pitfalls, the total population, as confirmed by actual observations, was somewhat larger.

It seems reasonable to estimate an average of approximately 10 subadult and adult Side-blotched Lizards per acre in most favorable habitats, based upon plot samples and observations. Some less suitable habitats with fewer lizards would be offset by greater numbers of lizards in optimal areas and during favorable years, especially following optimum rainfall. Tinkle (1967:172) estimated the average adult density in Texas as 14 resident adults per acre, which dropped to eight in August, whereas in Colorado, *Uta* was estimated as 10–17 adults per acre.

A conservative estimate of the average maximum population of subadults and adults in the Monument is 3,828,000 *Uta stansburiana* per year. Estimates for each plant belt are: Pinyon (89,000 acres $\times$ 10 *Uta*) = 890,000; Yucca (172,800 acres $\times$ 10 *Uta*) = 1,728,000; and Creosote Bush (242,000 acres $\times$ 5 *Uta*) = 1,210,000 lizards.

UTA STANSBURIANA FROM LOWER COVINGTON FLAT

We established a study plot consisting of one acre and the adjacent area in the Monument uplands of Lower Covington Flat, at an elevation of 4600 feet (1402 m). The plot slopes slightly eastward and the loamy-sandy soil is devoid of any large rocks. It is in the Pinyon plant belt (Miller and Stebbins, 1964) and the major vegetation consists of Joshua Tree (*Yucca brevifolia*), California Juniper (*Juniperus californica*), shrubs such as California buckwheat, Great Basin Blue Sage (*Salvia carnosa*), Mormon Tea (*Ephedra*), and needle grass (*Stipa*). The area is at the southern edge of the Mojave Desert region. In addition, the study plot had a 7-day recording hygrothermograph, a 31-day thermograph, a soil thermometer, a pyroheliometer, and several rain gauges.

Fifty-four cans, of three or five gallons, were buried flush with the surface and the open top was covered with a slightly elevated solid lid. Forty-one of these pitfalls were spaced throughout the acre plot, seven others were located adjacent to it, and six cans were buried among nearby rocks. These served as continuously operating traps which captured many small reptiles, mammals, and arthropods. The vertebrate most frequently captured was *Uta stansburiana* although six other lizards, three kinds of snakes, and ten species of mammals also were taken during nearly four years of continuous operation. The cans were checked nearly every week except for less frequent winter examinations.

The vertebrates were carefully examined, samples of ectoparasites were preserved, and the total number, sites of attachment, and color of the chiggers were recorded. Each individual vertebrate was measured, recorded, and, if alive and active, was marked and released at the site of capture. All information about each capture was recorded on a punched card, and all cards were assembled for rapid retrieval of data.

More than 15 species of chiggers were taken from vertebrates in and adjacent to the study plot. Five kinds of chiggers were found on *Uta*, and three of these, *Neotrombicula harperi* (Ewing), *Euschoengastoides longitarsala* (Powder and Loomis), and *Odontacarus arizonensis* (Ewing), were common. The names of the chiggers usually follow those listed in Gould (1956) and Brennan and Jones (1959) although *Eutrombicula* and *Neotrombicula* have been

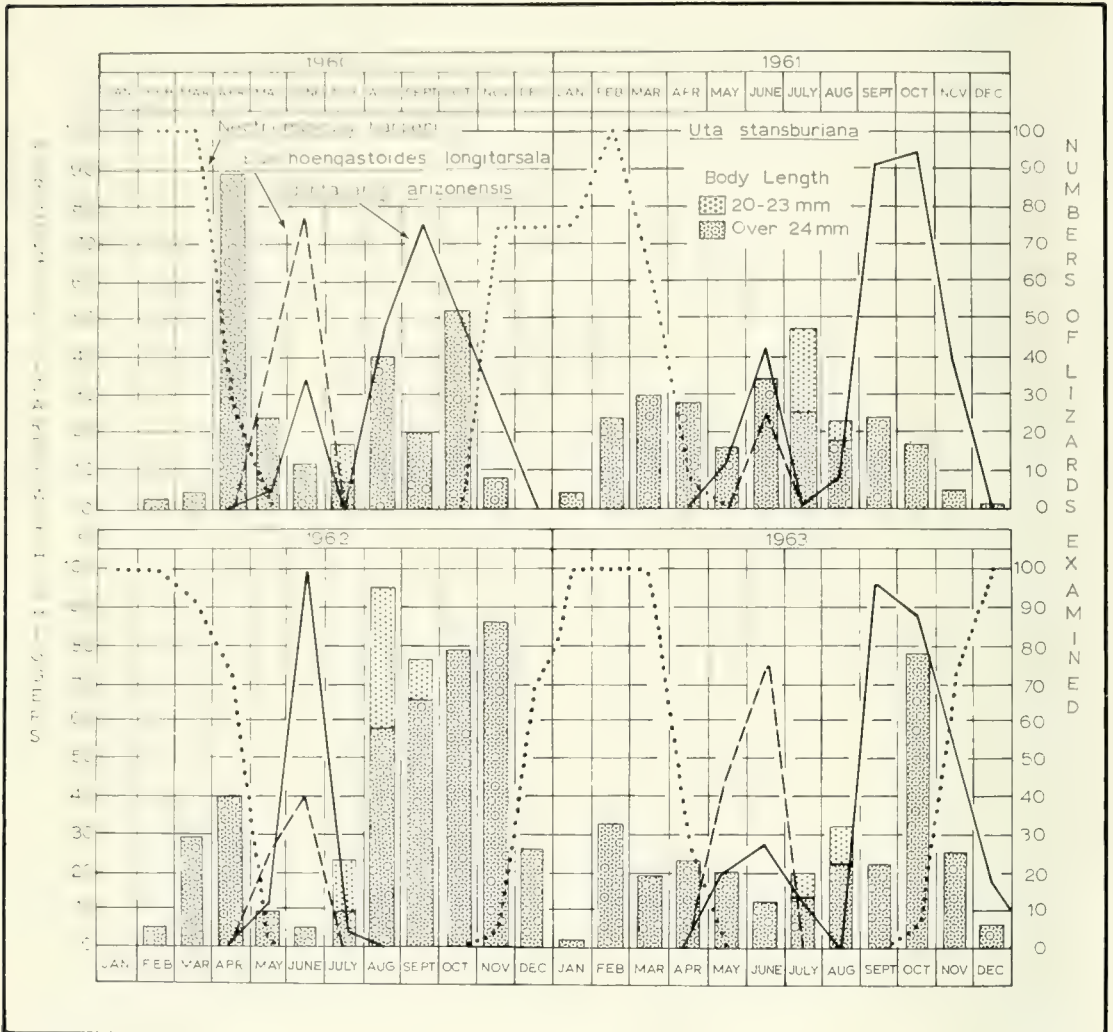


Figure 2. The Chiggers on *Uta stansburiana* in and adjacent to the Study Plot for each of the four years (1960–1963). The records for the chiggers and the lizards are arranged by month. The number of lizards is shown as a bar. Most of the lizards in July to October are small and the hatchlings are indicated separately. Note the absence of *Odontacarus arizonensis* in the fall of 1962.

elevated to generic rank (Vercammen-Grandjean, 1960). We have tentatively assigned *Euschoengastia longitarsala* Powder and Loomis (1962) to the genus *Euschoengastoides*, *sensu lato*. In addition, *Hexidionis lacerticola* (Loomis) follows Lucas and Loomis (1968). Finally, we have used the name *Neotrombicula harperi* (Ewing) for the larva taken from lizards in southern California even though they probably represent a new, but closely similar species. Each species of chigger had its own sites of attachment and a

different seasonal occurrence and abundance of the larvae.

Results of four year study.—The survey of lizards and their ectoparasites was conducted continuously for four years from 1960 through 1963. We have summarized this information on *Uta stansburiana* and its chiggers for each month on four graphs (Fig. 2) each representing a single year, and one graph (Fig. 3) combines these four years. The total of 1314 Side-blotched Lizards examined included recaptures as well

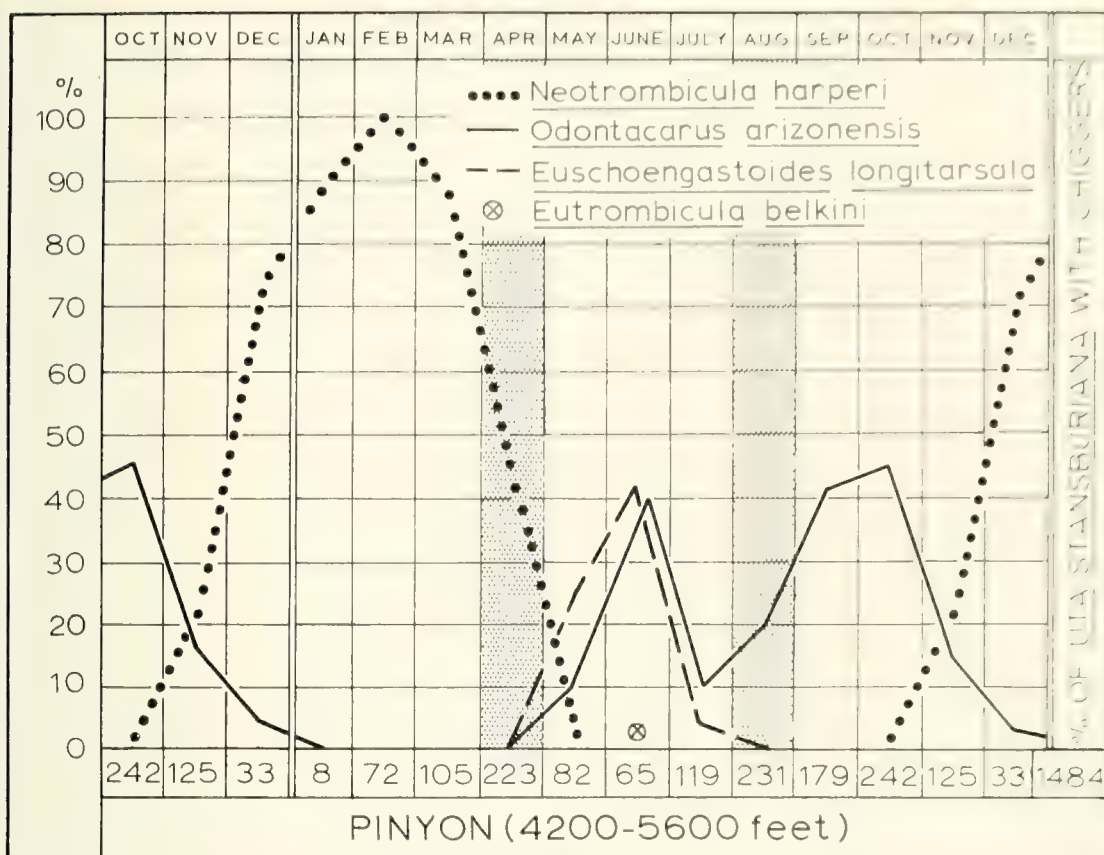


Figure 3. The seasonal occurrence and abundance of four species of chiggers on *Uta stansburiana* in the Pinyon Plant Belt of Joshua Tree National Monument (1959–1966). The presence of larvae on the lizards was calculated by month. April and August are shaded, and October through December are repeated for continuity. The numbers of individual lizards examined each month and the total for each plant belt are shown in the lower row.

as those taken within and adjacent to the acre plot. We excluded any lizard recaptured immediately or one which was dead and decayed.

Ninety percent of all records are from the acre plot, with 98 percent from July to March as compared to only 78 percent from March to July. The smaller percentage of *Uta* from the plot in the spring reflected our seasonal sampling of available lizards from outside the plot.

The presence or absence of each kind of chigger on each *Uta* has been recorded and these data were used to determine the occurrence and abundance of the larvae. Also we can surmise that the unfed larvae emerged and attached several days to weeks prior to recovery in all months except in late winter and early spring (January through March).

Each of the three species of chiggers appeared

approximately the same time each year. The graphs show the percentage of occurrence of each species of chigger on all *Uta* examined during that month. A positive host had at least one chigger but we have found a positive correlation of abundance with percentage of occurrence. The bars represent the numbers of lizards examined. The tiny hatchlings (indicated by dark shading) had very few chiggers attached. The juveniles represent the great majority of the lizards in the months of July and August. In July, chiggers were on 21 percent of the adults, but only on one percent of the juveniles. Later in the year the juveniles increased in size and picked up more chiggers. All of the lizards were adults or subadults in February through June, and the sampled numbers and actual population size reached a low in June.

Comparison of sexes revealed no differences in chigger attachment.

Neotrombicula harperi (Ewing) was found attached on the host from October to April, with the peak of abundance in February. A large percentage of the few lizards taken in the winter had these red larvae on the upper eyelids (Fig. 1) and all were engorged in February through April, suggesting that the larvae remain attached for one, two, even three months. A few larvae of *Odontacarus arizonensis* were occasionally present with *N. harperi* from October to early December.

Euschoengastoides longitarsala (Powder and Loomis) was taken only in May and June and the orange larvae usually were found in the lateral nuchal fold. The study plot is near the eastern margin of its known range. It was frequently found with the chiggers listed below (see Fig. 6), but it was recognized, when engorged, by its larger size and the absence of red pigment around the idiosomal ganglion.

Odontacarus arizonensis (Ewing) was the most common chigger on *Uta stansburiana* and it had the longest period of larval activity, usually from May to November. It overlapped both *N. harperi* in the late fall and *E. longitarsala* in the spring. The sites of attachment included the lateral nuchal fold, the axillae, groin and base of the tail, as shown in Figure 1. The larvae seemed to attach farther back as the season progressed, possibly because the anterior sites became unsuitable, due to damage caused by earlier chigger attachment. The larva was light orange to yellow with a bright red ventral ganglion and when engorged was the smallest of the chiggers.

Comparison of the chigger activity in four years.—Certain differences became evident when the four years were compared. In 1962, there was a peak abundance of *Odontacarus arizonensis* in June (although only five adult lizards were examined) followed by a complete absence of larva in August through December. Normally this is the period of greatest abundance of *O. arizonensis*. Since there were more lizards examined by the same experienced field workers in 1962 than during any other year, the absence of chiggers was not the result of inadequate or improper sampling.

Analysis of temperature and rainfall data, nearly complete for the plot from late 1960 to early 1963, revealed the following. The average of daily temperatures during the spring and summer of these years were similar although it was

slightly higher in 1962 than in 1961. Since these chiggers occur throughout the desert in hotter situations, this slight change could not be considered enough to eliminate larval activity. The rainfall, however, seemed to be the key to the difference. In the area of the study plot, most precipitation falls in the winter as rain or snow. Usually the rainfall from November through March is over four inches; however, in 1961–62 it was greater (5.5 inches) as compared to 2.3 inches in 1960–61 and 4.5 inches in 1962–63. The summer usually has only scattered rainfall. In 1961, there were three months without rain (April–June); but in 1962, six months (April–September) were extremely dry, with only 0.08 inch in early April. The heavy rains in early spring seemed to provide optimum moisture for incubation and hatching of a record number of *Uta* eggs, but the lack of rainfall through the next six months resulted in a prolonged drought which apparently caused the complete disappearance of *Odontacarus* larvae from *Uta* and from all other lizards in the plot area. In addition, the population of *Uta* declined rapidly through the rest of the year. However, this long dry period in 1962 did not eliminate *Odontacarus arizonensis* from the plot as they appeared in abundance the following year, suggesting that the dry period greatly affected only the egg deposition and unfed larvae of late 1962.

The difference in chigger abundance on hosts in 1962, as compared with other years, points out the danger of using samples from only one year, or taking the total of each month for several different years to depict correctly the seasonal occurrence and abundance of larvae of any species.

UTA STANSBURIANA FROM THE ENTIRE MONUMENT

We summarized all of the information on the chiggers from *Uta stansburiana* of the Monument. Five species of chiggers occur regularly, including *Eutrombicula belkini* (Gould) and *Hexidionis lacerticola* (Loomis) in addition to the three species from the plot area. The data have been arranged by altitudinal plant belts (Pinyon, Yucca or Creosote Bush) to illustrate the differences in species and times of larval emergence.

The majority of our chigger records from *Uta* were from the Pinyon plant belt, and most of

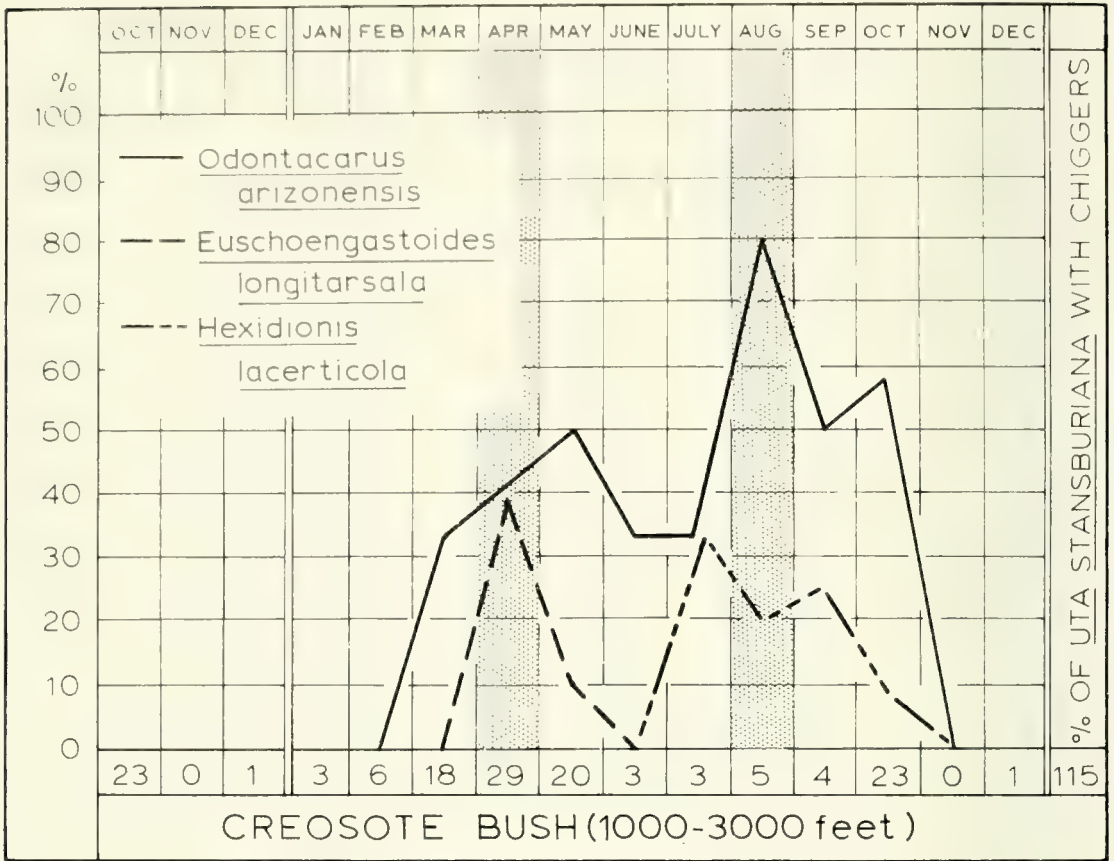


Figure 5. The seasonal occurrence and abundance of three species of chiggers on *Uta stansburiana* in the Creosote Bush Plant Belt of Joshua Tree National Monument (1959-1966). See legend of figure 3 for further explanation of figure.

August. *Hexidionis lacerticola* first appeared in July and had a peak in October. *Odontacarus arizonensis* occurred from May (few) through November, with one peak in June, a decline in July followed by a second peak in August.

Spoecker (1967) reported four species of chiggers on *Uta stansburiana* from the Mojave Desert, approximately 125 miles northwest of Joshua Tree National Monument. He utilized pitfall traps arranged in several lines on a slope from 3600 to 4100 feet in elevation. The chiggers were more abundant in the highest line which he attributed to more moisture retained in the soil, and not merely to a difference in elevation. Three of these species, *Odontacarus arizonensis*, *E. longitarsala* and *E. belkini*, also were found in Joshua Tree National Monument, whereas the fourth, *Neotrombicula* sp. is similar to *Neotrombicula harperi*. He found that *Neotrombicula* on the upper eyelids occurred in November to

May, and tail mites (*Odontacarus arizonensis*) were present as two peaks, one May and June and the second from August through December. He indicated a drop in *O. arizonensis* in July for both years. This is coincident with Hunter (1966) and with our results.

OTHER LIZARDS IN THE MONUMENT

All of the kinds of chiggers found on *Uta stansburiana* were attached regularly only on lizards in the Monument. Therefore we have summarized all of the lizards sampled and the incidence of chiggers.

Seventeen species of lizards are known from the Monument, and samples of these lizards have been examined for chiggers. Only four species were negative: *Xantusia vigilis*, Desert Night Lizard (114 individuals); *Uma scoparia*, Mojave Fringe-toed Lizard (30 lizards); *Sauro-*

TABLE 2. The lizards from Joshua Tree National Monument examined for chiggers (1959-1966) and the occurrence and abundance of the five species of chiggers; A, *O. arizonensis*; B, *E. belkint*; C, *H. lacerticola*; D, *N. harperi*; E, *E. longitarsala*. The first column represents the number of lizards with larvae and the second column is the percent of occurrence on the lizards. Only those lizards examined during known larval activity are considered in the total.

Species of lizards	Totals	Species with chiggers				
		A	B	C	D	E
		No. (%)	No. (%)	No. (%)	No. (%)	No. (%)
<i>Uta stansburiana</i>	744	300 (20)	4 (1)	19 (24)	326 (38)	78 (22)
	1703					
<i>Sceloporus occidentalis</i>	67	26 (19)	3 (3)	3 (6)	24 (29)	12 (12)
	233					
<i>Cnemidophorus tigris</i>	24	10 (11)	6 (7)	1 (3)	0	0
	122					
<i>Callisaurus draconoides</i>	18	17 (23)	0	1 (6)	0	0
	80					
<i>Sceloporus magister</i>	19	13 (31)	1 (8)	4 (19)	0	7 (22)
	55					
<i>Dipsosaurus dorsalis</i>	11	10 (33)	0	0	0	2 (20)
	39					
<i>Phrynosoma coronatum</i>	5	3 (38)	0	0	0	2 (9)
	37					
<i>Phrynosoma platyrhinos</i>	12	12 (44)	0	1 (17)	0	7 (29)
	27					
<i>Crotaphytus wislizeni</i>	12	10 (45)	0	3 (30)	0	4 (29)
	25					
<i>Crotaphytus collaris</i>	9	9 (70)	0	1 (25)	0	4 (44)
	13					
<i>Urosaurus graciosus</i>	2	2 (20)	0	0	0	0
	15					

malus obesus, Chuckawalla (19 specimens); and *Anniella pulchra*, California legless lizard (1 example). Samples of these lizards from outside the Monument also lacked chiggers. Two other lizards, *Coleonyx variegatus*, Banded Gecko (51 samples) and *Eumeces gilberti*, Gilbert's skink (30 specimens) possessed chiggers, but they are species not found on *Uta stansburiana*, and therefore are not considered further. Thus eleven species of lizards were hosts for one or more species of chiggers also found on *Uta*. Table 1 gives the numbers of these 11 kinds of lizards examined by month, and whether or not each individual had chiggers. The occurrence

and abundance of each kind of chigger on each species of lizard can be found in Table 2.

Ten of these 11 lizards are iguanids, a family containing many genera and species which are abundant throughout North America. The other lizard, *Cnemidophorus tigris*, belongs to the family Teiidae, which has many other genera and species in South America. All of the host lizards are modest in size, the adults ranging from 44 to 125 mm snout-vent. Both the largest (*Sauromalus obesus*, up to 200 mm) and the smallest lizard (*Xantusia vigilis*, adults, 37 to 44 mm) lacked chiggers.

The presence of one or more kind of chig-

	CHIGGERS				
	1	2	3	4	5
1	307	38	10	4	8
2	79	17	1	4	0
3	23	14	4	0	0
4	10	1	3	0	0
5	2	3	0	5	0
6	0	0	0	0	326
7	0	0	0	0	24
OTHER LIZARDS					J T N M

Figure 6. The frequency of parasitized lizards with one or two species of chiggers. This chart gives the number of lizards from Joshua Tree National Monument, parasitized by one or two species of chiggers and indicates which kinds occurred together. To determine the incidence and how many were found alone or with another species of chigger, trace the horizontal column until it intersects each vertical column. Figures above and to the right of the center divider are for *Uta stansburiana* and those numbers below and to the left are the totals for the ten other species of lizards. The total number is 883; 719 from *Uta stansburiana* and 164 for the other lizards.

gers on a host depends on several factors: 1) Season of larval activity, 2) geographic distribution, 3) ecological conditions and, 4) host selection and specificity. The records of the five chiggers found regularly were arranged in Figure 6 and these numbers are analyzed below.

Neotrombicula harperi, the only cool weather chigger, was found alone in 98 percent of the samples, with only two percent coincidence with *Odontacarus arizonensis* as the latter disappeared in late fall and early winter. Therefore, the difference in seasonal activity accounts for the virtual absence of other chiggers with *N. harperi*.

The remaining four species are warm weather chiggers. *Odontacarus arizonensis* is the most common with the greatest distribution and longest season of larval activity. Eighty percent of the lizards with chiggers had only *O. arizonensis*. Since virtually all of the chiggers found together were with *O. arizonensis* (91 percent), each species will be compared to it.

Euschoengastoides longitarsala was alone in 31 percent of the collections, and 61 percent of the coincidence was with *O. arizonensis*, reflecting the complete seasonal overlap of *E. longitarsala* with *O. arizonensis*.

Eutrombicula belkini was taken occasionally in the Monument and it was alone in 28 percent of the records. Because of the few records, the coincidence with other chiggers was not figured.

The last species, *Hexidionis lacerticola*, was alone only 21 percent of the time, and 60 percent of the other collections were with *O. arizonensis*. Only two lizards possessed both *H. lacerticola* and *E. longitarsala*.

In summary, there were four warm weather and one cool weather species of chiggers. There was virtually no overlap (two percent) between these two groups. Among the four warm weather chiggers the most abundant species, *Odontacarus arizonensis*, overlapped the other three in seasonal activity and geographic distribution and it was represented in nearly all of the examples of coincidence (91 percent).

EXAMINATION OF OTHER VERTEBRATES FROM THE MONUMENT

We have examined all of our records of chiggers to determine if the five species of chiggers are found on hosts other than *Uta stansburiana* and other lizards in the Monument. A brief summary of these records follows.

Approximately 4600 vertebrates taken from many localities throughout the years of 1959 through 1966 have been examined for chiggers. Two kinds of amphibians (136 frogs and toads) were examined and nearly 80 were infested only with chiggers of the genus *Hannemania*. A total of 124 snakes were checked and 21 of these had chiggers, none of which were those reported from lizards.

More than 200 birds of many kinds were examined from the area around the study plot in Covington Flats and no chiggers were found. The only locality where birds possessed chiggers was Cottonwood Spring which had moist surface soil surrounding a watering site. Of approximately 74 birds examined, four had chiggers; one had two *Eutrombicula belkini* and another bird had one *Hexidionis lacerticola*.

Nearly 1700 small mammals were examined for chiggers and more than 900 of them had chiggers. Of 860 rodents with chiggers, two pocket mice (*Perognathus formosus*) had *Eu-*

trombicula belkini (3 larvae). Of 131 bats examined, 54 had chiggers of other species.

It is concluded that none of these five species of chiggers (*Neotrombicula harperi*, *Eutrombicula belkini*, *Hexidionis lacerticola*, *Euschoenogastoides longitarsala*, and *Odontacarus arizonensis*) regularly occurs on vertebrates other than lizards in the Monument. Except for *Eutrombicula belkini* previously reported from snakes, birds and mammals (Gould, 1956), the records of these chiggers from hosts other than lizards probably were the result of numbering errors or mixing of chigger samples before or after slide preparation.

SUMMARY AND CONCLUSIONS

Four species of chiggers (*Odontacarus arizonensis*, *Hexidionis lacerticola*, *E. longitarsala*, and *Neotrombicula harperi*) were common on *Uta stansburiana* and other lizards. They have become dependent on lizards after the adaptation of their life cycles to the activity and abundance of the hosts. They rarely if ever successfully parasitize other vertebrates.

Odontacarus arizonensis attached more posteriorly as the year progressed apparently because of scabs and scars in the anterior sites which made them unsuitable for continuous attachment. The two peaks of larval abundance seemed to be correlated with numerous hosts whereas the early summer decrease in larvae coincides with the reduction of available adult hosts and emergence of the tiny hatchlings. The absence of larvae in the late summer of 1962 was correlated with a long period devoid of precipitation.

ACKNOWLEDGMENTS

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and sample its flora and fauna, and to the naturalist and rangers for their assistance.

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NOTES ON BATS FROM THE MEXICAN STATE OF QUERETARO

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ABSTRACT. Records of 20 species of bats from the Mexican State of Queretaro are herein reported. Seven species (*Anoura geoffroyi*, *Choeronycteris mexicana*, *Sturnira ludovici*, *Desmodus rotundus*, *Myotis yumanensis*, *Pipistrellus hesperus*, and *Euderma maculatum*) are recorded from Queretaro for the first time. The range of the spotted bat, *Euderma maculatum*, is extended 575 air miles to the southeast from Navarro, Durango. Pertinent information regarding natural history of certain species is given.

Queretaro is interesting biogeographically because the southwestern portion of the state lies on the Mexican Plateau whereas the northern portion is associated with the western slopes of the Sierra Madre Oriental. Consequently, it has a variety of different ecological situations, including tropical deciduous and tropical evergreen forests at the easternmost edges of the state, the pine-oak forests of the numerous scattered montane areas and xeric, thorn shrub, and desert in the northern and southern areas.

Perusal of the pertinent literature reveals but few scattered reports and observations concerning the distribution and natural history of bats in Queretaro. Nelson and Goldman made a collection of bats from Jalpan on August 25, 1896 (Don E. Wilson, pers. comm.). It included nine *Antrozous pallidus* (USNM nos. 81621–81628), seven *Leptonycteris sanborni* (81629–81635), five *Tadarida brasiliensis* (81636–81640), and two *Myotis velifer* (81641–81642). H. O. Wagner collected three specimens of *Antrozous pallidus* (Univ. Michigan Mus. Zool. nos. 93559–93561) at Cadereyta, 2100 m, on July 17, 1948 (Emmet T. Hooper, pers. comm.). Malaga Alba and Villa-R. (1957) evidently were the first to publish records of bats from the state when they reported *Antrozous pallidus pallidus* from Jalpan and Cadereyta. Hall and Kelson (1959) list only the record reported by Malaga Alba and Villa-R.; they indicate that several chiropteran species possibly occur in Queretaro but they list no specimens examined for any of them. In his monograph on the bats of Mexico, Villa-R. (1967) mentioned the earlier record of *Antrozous* and listed specimens of *Leptonycteris nivalis*, *Lasiurus borealis*, *Antrozous pallidus*, and *Tadarida brasiliensis*. Davis (1969, 1970) first recorded fruit bats, *Artibeus jamaicensis yucatanicus* and *Artibeus aztecus aztecus*, from Quere-

taro. Finally, Spenrath and LaVal (1970) reported *Pteronotus personatus*, *Glossophaga soricina*, *Sturnira lilium*, *Artibeus lituratus*, and *Molossus ater* from the vicinity of Jalpan in northern Queretaro. Thus, a total of 13 species of bats representing four families are on record.

From 1970 to 1972 several field expeditions to Queretaro were conducted by personnel of the Department of Wildlife and Fisheries Sciences, Texas A and M University. These trips resulted in the capture of 134 bats from six different localities in the state—several places near (1) Jalpan and (2) El Lobo in northern Queretaro; (3) Pinal de Amoles, (4) Peña Blanca, and (5) San Joaquin in the central part of the state; and (6) Rio Galindo in the southern sector. The vegetation at Jalpan, El Lobo, Pinal de Amoles, and Peña Blanca is described by Dixon, Ketchersid, and Lieb (1972) in their account of the herpetofauna of Queretaro. San Joaquin is on the eastern edge of the Mexican Plateau in east-central Queretaro. The vegetation consists of drooping-needle pine, juniper, acacia, and madrona which cover the dry rocky canyons of the area. The Rio Galindo is a small river one-half mile south of Hacienda Galindo at 6500 ft. Tall cypress trees overhang the river; the major plants along the banks include agave, mesquite and other thorny shrubs, and willow trees. Among the specimens thus accumulated are 15 species of bats, seven of which are new to the fauna of the state. In the accounts beyond, which include all of our Queretaro specimens, measurements are in millimeters and all place-names refer to localities in Queretaro.

Glossophaga soricina leachii (Gray, 1844).—six females were netted in a banana grove at

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Hacienda X-Conca, 2 mi SSE Conca (16 mi NNW Jalpan), 2000 ft, on 29 December 1970. On 4 January 1972, five females and one male were collected at this same locality. None of the female specimens collected evidenced gross reproductive activity. Other species captured at Hacienda X-Conca on the dates mentioned included *Anoura geoffroyi*, *Sturnira lilium*, *S. ludovici*, *Desmodus rotundus*, *Artibeus literatus*, and *Molossus ater*.

Anoura geoffroyi lasiopyga (Peters, 1868). One male and one female were netted 1.9 mi W El Lobo, 5400 ft, and at Hacienda X-Conca on 4 June 1970 and 29 December 1970, respectively. The specimen from El Lobo was netted over a small sink hole. These specimens represent the first records of occurrence for this species from Queretaro. The nearest locality is 5.6 km NW Xilitla, San Luis Potosi (Spenrath and LaVal, 1970).

Choeronycteris mexicana Tschundi, 1844.—One male specimen was collected 5 August 1972 at a place 12.4 mi WSW San Joaquin. This specimen, along with one *Artibeus aztecus*, was captured at the bottom of a dry rocky canyon covered with drooping-needle pine, juniper, acacia, and madrona. This specimen represents the first record of this species from the state.

Leptonycteris sanborni Hoffmeister, 1957.—On 19 May 1972, a male was obtained over a shallow pool near a steep cliff on the banks of the Rio Extoras, 1 mi NE Peña Blanca, 4450 ft. The Peña Blanca area supports desert vegetation with a small gallery forest of trees confined to the banks of the river. Other bats collected at this same locality include *Desmodus rotundus*, *Pipistrellus hesperus*, *Tadarida brasiliensis*, and *Euderma maculatum*. Another specimen, a male, was captured in a dry stream bottom in an area where sweet gum, oak, walnut, and several lush shrubs are the dominant vegetation 7 mi ENE Pinal de Amoles, 6000 ft. These two specimens represent the first published records of *L. sanborni* (as defined by Davis and Carter, 1962) from Queretaro. The average length of the third metacarpal, and the first, second, and third phalanges of the third digit of our two specimens are 50.1, 14.1, 23.8, and 10.4, respectively.

Sturnira lilium parvidens Goldman, 1917.—Specimens were netted at the following localities: Hacienda X-Conca, 5(2 females, 3 males); 2 mi NW Conca, 5(4 males, 1 female); 7 mi ENE Pinal de Amoles, 2 females; and Rio Galindo, 1 male. The specimens from the vicinity of

Conca and Pinal were obtained in habitat discussed in the accounts of *Glossophaga soricina leachii* and *Leptonycteris sanborni*, respectively. The specimen at Rio Galindo was netted over a deep pool of water under large cypress trees. None of the females evidenced reproductive activity.

Sturnira ludovici ludovici Anthony, 1924.—Twenty-one specimens (12 males, 9 females) were netted at Hacienda X-Conca on 4 and 5 January 1972. On 5 January, two females were netted 2 mi NW Conca. These specimens constitute the first records for Queretaro. None of the females showed signs of reproductive activity.

Artibeus jamaicensis yucatanicus J. A. Allen, 1904.—Two females were netted over a small pool of water in a rocky stream bottom 5 January 1972, 2 mi NW Conca, 2300 ft. Other bats obtained at this site were *Sturnira lilium*, *S. ludovici*, *Artibeus lituratus*, and *A. aztecus*. Twenty specimens (9 males and 11 females) were also collected at Hacienda X-Conca under conditions reported earlier in this report. None of the females at either locality evidenced signs of reproductive activity.

Artibeus aztecus aztecus Andersen, 1893.—Seven specimens (3 males and 4 females) were captured on 5 January 1972 at 2 mi NW Conca, 2300 ft, in habitat previously discussed for *A. jamaicensis yucatanicus*. Three specimens (2 males and 1 female) were caught at Hacienda X-Conca and another male was collected 12.4 mi WSW San Joaquin. None of the females showed evidence of reproductive activity. The only other record of this species from Queretaro is from 20 mi E Landa, 5400 ft (Davis, 1969). The elevations at which our specimens were taken apparently represent the lowest recorded for this species. Previously, *A. aztecus* had not been recorded at elevations lower than 3300 ft (Davis, 1969).

Artibeus lituratus palmarum J. A. Allen and Chapman, 1897.—Two females were obtained at Hacienda X-Conca in habitat discussed in the account of *Glossophaga soricina leachii*. Three specimens (2 females and 1 male) were obtained 2 mi NW Conca in habitat described in the account of *A. jamaicensis yucatanicus*. The females evidenced no sign of reproductive activity.

Desmodus rotundus murinus Wagner, 1840.—Vampire bats have not previously been recorded from Queretaro. On 5 and 7 June 1970, nine specimens (7 males and 2 females) were captured 10 mi N Jalpan in nets set across the Rio

Jalpan. One of the females was pregnant (embryo 22 in the crown-rump length); four of the males had scrotal testes. On 29 December 1970, D. W. Coon netted 5 males and 5 females at Hacienda X-Conca. In these specimens, the testes of the males were scrotal and the uteri of three females were swollen. On 17 May 1972 seven vampires (4 females and 3 males) were obtained 1 mi NE Peña Blanca. One of four females was pregnant (embryo 41 in crown-rump length). Apparently vampire bats are common throughout Queretaro and breed throughout the year.

Myotis yumanensis lutosus Miller and G. M. Allen, 1928.—Two females were obtained on 21 May 1972 at Rio Galindo. These specimens represent the first record for Queretaro.

Pipistrellus hesperus maximus Hatfield, 1936.—Two males were captured 1 mi NE Peña Blanca. These represent the first record for Queretaro.

Euderma maculatum (J. A. Allen), 1891.—One specimen, a male with small abdominal testes, was obtained 1 mi NE Peña Blanca on 19 May 1972. This specimen, the first recorded from Queretaro, was netted over a shallow pool next to a steep cliff along the Rio Extoras. Only three other specimens of the spotted bat, all from Navarro, Durango (Gardner, 1965), have been reported from Mexico. Peña Blanca is more than 575 air miles southeast of Navarro. The occurrence of *Euderma* at this locality suggests this rare bat may occur throughout the Mexican Plateau. Measurements of our specimen are: total length, 139; length of forearm, 52.6; length of skull, 19.7; zygomatic breadth, 11.0; and cranial depth, 8.6.

Tadarida brasiliensis mexicana (Saussure, 1860).—On 19 May 1972, six adults (4 females, 2 males) were obtained 1 mi NE Peña Blanca. Three of the four females were pregnant (embryos 13, 12 and 7 in crown-rump length). The only other record of this species from Queretaro is a single specimen from San Juan del Rio (Villa-R., 1967).

Molossus ater nigricans Miller, 1902.—Five specimens (3 males, 2 females) were mist-netted under large cypress trees at Hacienda X-Conca on 4 January 1972; none of them evidenced reproductive activity. Spennath and LaVal (1970)

reported six additional specimens from the vicinity of Jalpan.

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COLUBRID SNAKES OF THE GENUS *TANTILLA* FROM NICARAGUA

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ABSTRACT: Five species of the colubrid snake genus *Tantilla* are now known from Nicaragua. With the exception of *T. annulata* (not reported from Nicaragua since its original description) all known species of the genus are treated here. A key for the identification of all Nicaraguan species of *Tantilla* is provided.

Members of the snake genus *Tantilla* are infrequently reported from Nicaragua, both because of the paucity of published work on the herpetofauna of that country in general and the seeming difficulty in obtaining these secretive snakes. We have examined all available specimens of all but one species of *Tantilla* (*T. annulata*) reported from Nicaragua. *Tantilla annulata* has not been reported from Nicaragua since its original description (Boettger, 1892). A key for the identification of all five species of *Tantilla* known from Nicaragua is provided below. The following information will help to some degree to fill in the gaps in our knowledge concerning Central American *Tantilla*.

We are grateful to William E. Duellman, Museum of Natural History, University of Kansas (KU), James A. Peters, United States National Museum (USNM), and Charles F. Walker, University of Michigan Museum of Zoology (UMMZ) for the loan of specimens. The junior author's material (JV) will be deposited in the KU collection. We would also like to thank Kraig Adler for his critical review of the manuscript.

Tantilla armillata Cope

Hardy and Cole (1967) reported the first specimen of *T. armillata* from Nicaragua (collected on Isla de Ometepe, Lago de Nicaragua, Depto. Rivas). We now report fifteen additional specimens: "Nicaragua" (USNM 11257, 15205, 16128, 25241; all but USNM 11257 are females); "Managua" (USNM 89478, male; presumably from the city); DEPTO. CHONTALES, Juigalpa (JV 753, female); DEPTO. MANAGUA, Los Robles (JV 620, female); DEPTO. MATAGALPA, 0.3 km W Matagalpa, 455 m (UMMZ 116515-2 spec., a pair), 0.6 km W Matagalpa, 758 m (UMMZ 116514, male), 0.9 km N Mata-

galpa, 909 m (UMMZ 116516-2 spec., a pair), 1.3 km N Matagalpa, 606 m (UMMZ 116517, female); DEPTO. RIVAS, 12 km N Costa Rican border between Pan American highway and Lago de Nicaragua (KU 140077, female), Finca Amayo, 13 km S, 14 km E Rivas, 40 m (KU 101922, female) (Fig. 1). In the following discussion data are included for the specimen reported by Hardy and Cole (1967).

The specimens have 15 dorsal scales throughout, 7 supralabials, and 1+1 temporals. The preocular and postnasal are excluded from contact with one another in all specimens. The preocular is absent on the right side of the head in UMMZ 116516 and the prefrontal thus enters the orbit. All specimens except UMMZ 116514 have two postoculars on both sides; UMMZ 116514 has the postoculars fused on the left side. The specimens have 6 infralabials except for UMMZ 116514, which has 5 on both sides. The first pair of infralabials is in contact with one another in 14 specimens but not in two others. Total length ranges from 95 to 268 mm. One specimen (UMMZ 116517) has a truncate tail but has a snout-vent length of 250 mm, surpassing by 45 mm the snout-vent length of the largest complete specimen.

Variation in ventrals and subcaudals is great for the ten female *armillata* and relatively restricted for the six males. Ventral counts range from 148 to 173 in females (mean, 164.1) and 155 to 166 in males (mean, 161.0). Subcaudal counts range from 44 to 59 in females (mean, 48.1) and 50 to 56 in males (mean, 53.0).

The basic dorsal pattern in *T. armillata* consists of a dark brown longitudinal stripe occupy-

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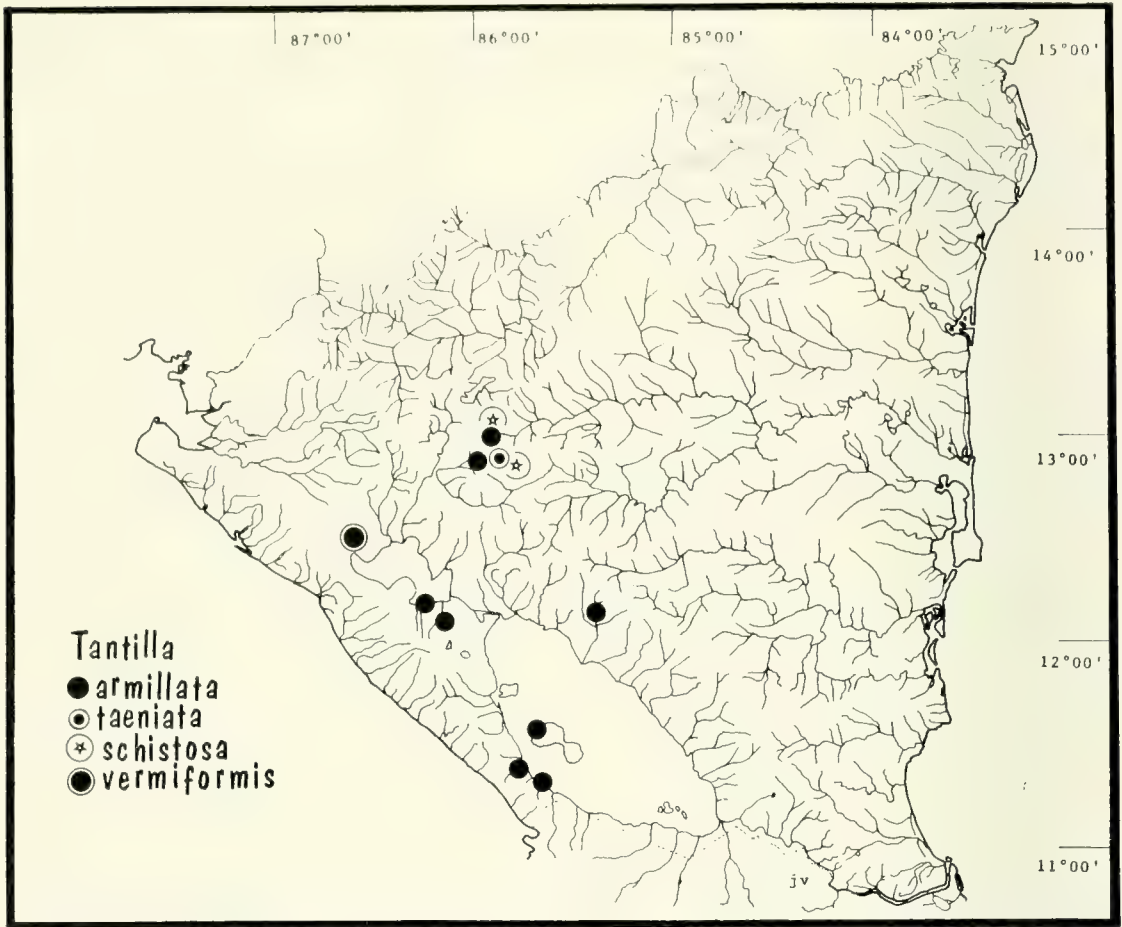


Figure 1. Distribution of four species of the colubrid genus *Tantilla* in Nicaragua.

ing the middle of the middorsal row of scales and a pale cream longitudinal stripe on the adjacent halves of rows 3 and 4 on a brown ground color. Specimens from Nicaragua show trends away from this basic pattern in two directions; toward accentuation and toward diminution of the pattern. In some specimens (especially USNM 15205) the middorsal stripe is relatively broad and well-defined, the lateral stripe is accentuated by an outline of dark brown pigment and the area below the pale lateral stripe appears striped as well because of concentration and intensification of dark pigment in the center of scale rows 1 and 2. On the other hand, there are specimens (e.g., JV 620 and 753) in which the dark middorsal stripe is relatively narrow and less well-defined and the pale lateral stripe has almost blended in with the surrounding groundcolor (at least at midbody and beyond).

The head pattern varies as well. Basically, the head pattern of *T. armillata* consists of a dark head cap extending posteriorly onto the nape a distance of from 4 to 6 scales posterior to the parietals. On the dorsum of the head there is a spot on the rostral and internasals, small spots at the junction of the supraocular, frontal, and parietal scales, spots at the posterolateral edge of the parietals, and paravertebral spots at the posterodorsal edge of the nuchal band. On the side of the head there is a preocular and postocular spot, a dorsal extension of the pale gular coloration onto the last supralabial (in line with the parietal spots) and lateral spots at the posterolateral edge of the nuchal band (in line with the paravertebral spots). The principal variation on this theme involves the fusion of the dorsal and lateral postnuchal spots on each side (the middorsal dark stripe is confluent with the dark nuchal band and separates

the postnuchal spots on one side from those on the other). In USNM 15205, however, the spots on the side of the head are largely confluent with one another and enlarged as are those on the dorsum of the head, producing a predominantly light head as opposed to the predominantly dark head of typical *armillata*. Much the same kind of head pattern is seen in UMMZ 116517. These two specimens are the largest examined and perhaps the enlargement and fusion of pale head spots is something that occurs in large specimens.

The specimens collected by the junior author were in dry deciduous forest, one was found at night, the other during the day under a rock.

Tantilla schistosa (Bocourt)

We have examined two specimens of *T. schistosa*, representing the first records for the country. One specimen (KU 86247) is a male from an elevation of 960 m at Finca Tepeyac, 10.5 km N and 9 km E Matagalpa, DEPTO. MATA-GALPA and the other (UMMZ 116525) is a female from about 697 meters at a point 19 km N Matagalpa, DEPTO. MATA-GALPA (Fig. 1). They have the following counts and measurements (data for KU 86247 listed first): ventrals 142, 147; subcaudals 31, 29+; supralabials 7-6, 7-7; infralabials in both 5-5, first pair widely separated from one another by contact of mental and anterior chin shields; preocular single and in contact with postnasal in both; postoculars 2-2 in both; temporals 1+1 in both; total length, 111 mm, 176+ mm; tail length, 14 mm, 24+ mm; tail length-total length ratio, 0.226, ?.

Smith (1962) reviewed this species and recognized four subspecies. He considered the nominate subspecies to range from Guatemala to Panamá and to be characterized by the presence of a nuchal collar throughout life, 123 to 136 ventrals and 31 to 40 subcaudals in males, and 128 to 138 ventrals and 24 to 37 subcaudals in females. The Nicaraguan specimens possess a nuchal collar which is light brown in color, extending in KU 86247 from the posterior portion of the frontal to a point 2 scales posterior to the parietals and in UMMZ 116525 from the middle of the parietals to a point one scale posterior to the parietals. The number of subcaudals in the male is at the lower limit of the range for male *T. s. schistosa*, but the ventral counts for both are far outside of the range for this subspecies and within that for either

T. s. phrenetica (Veracruz and Oaxaca, México) or *T. s. costaricensis* (central Costa Rica). In view of this inconsistency, we prefer to use only the specific epithet.

Tantilla taeniata (Bocourt)

In their revision of the *Tantilla taeniata* group, Wilson and Meyer (1971) were able to examine only nine specimens of *T. taeniata*, which has a range extending from Oaxaca, México to Nicaragua. Since that time an additional Nicaraguan specimen has been found.

The specimen (JV 7218) was collected in Matagalpa, DEPTO. MATA-GALPA (Fig. 1) and presented to the junior author. The area is about 1000 to 1200 meters in elevation, covered at one time by coffee groves, now somewhat cleared but still humid. The snake came from beneath a rock in moist earth. It is a female with the following counts and measurements: ventrals 161; subcaudals 62; supralabials 7-7; infralabials 6-6, first pair in contact behind mental; preocular single and in contact with postnasal; postoculars 2-2; temporals 1+1; total length, 320 mm; tail length, 78 mm; tail length-total length ratio, 0.244. All these counts and measurements fall within the known ranges of variation for this species (Wilson and Meyer, 1971). The color pattern is the same as that described for other specimens. The collar is complete and is two scales long.

The locality for this specimen of *T. taeniata* is about 175 km WSW of the other known locality in Nicaragua and about 190 km SE of the nearest locality in Honduras (Wilson and Meyer, 1971).

Tantilla vermiformis (Hallowell)

Tantilla vermiformis has been known from only six specimens, four syntypes (USNM 32338-41), all in poor condition, and USNM 75711-12; all six are from "Nicaragua." We have examined these specimens and, in addition, are able to report on a fresh specimen with precise locality data.

This female specimen (JV 7178) is from Laguna Monte Galán, DEPTO. LEÓN (Fig. 1) and exhibits the following counts and measurements: ventrals 116; subcaudals 27; anal plate divided; supralabials 7-7; infralabials 6-6, first pair not in contact behind mental; preocular single and in contact with postnasal; postoculars

2-2; temporals 1+1; total length, 145 mm; tail length, 21 mm; tail length-total length ratio, 0.144.

The following description of the color pattern is partially based on notes taken on the living specimen and partially on the color in preservative: dorsum pink with a diffuse dark brown stripe occupying the middorsal row, this stripe becoming less distinct posteriorly but continuing to the end of the tail; venter immaculate pale pink; top and sides of head dark brown with a V-shaped light brown mark on the parietals; chin pale with brown markings on the infralabials. This description agrees in essential respects with that given by Boulenger (1896) for the types.

Variation in scutellation in the seven known specimens of *T. vermiformis* may be summarized as follows: ventrals in males 115-120 (mean, 117.3), in a single female, 120; subcaudals in males 26-27 (mean, 26.2), in the female, 22; supralabials 7-7; infralabials 6-6, first pair not in contact behind mental; preocular single and in broad to narrow contact with postnasal; postoculars 2-2; temporals 1+1; anal plate divided (Boulenger's, 1896, statement notwithstanding); total length, 141 to 145 mm; tail length, 19 to 21 mm; tail length-total length ratio, 0.134 to 0.144.

KEY TO NICARAGUAN SPECIES OF *TANTILLA*

1. a. Pale vertebral stripe present, occupying the middorsal row and adjacent halves of paravertebral rows, and extending the length of body and tail; pale lateral stripe on adjacent halves of rows 3 and 4; scales of lowermost row distinctly divided into dark upper and pale lower half *Tantilla taeniata*
- b. Pattern not as above; vertebral stripe, if present, dark 2

2. a. Dorsum with a series of narrow, vertical, pale, black-bordered blotches on each side of the body, generally alternating with a similar series on the other side of the body; these blotches are at least present on the anterior portion of the body *Tantilla annulata*
- b. No vertical pale blotches on dorsum 3
3. a. Dorsum essentially unicolor; a pale transverse nuchal band present on the parietals *Tantilla schistosa*
- b. Dorsum with a dark longitudinal stripe on the middorsal scale row; head markings variable 4
4. a. Head and nape dark in color, contrasting strongly with the paler dorsal groundcolor; ventrals more than 145; subcaudals more than 40 *Tantilla armillata*
- b. Head only slightly darker in color than dorsum of body, with a pale marking on the parietals; ventrals less than 125; subcaudals less than 30 *Tantilla vermiformis*

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EARTH RESOURCES TECHNOLOGY SATELLITE: A NEW RESEARCH AND RESOURCE MANAGEMENT TOOL

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The first Earth Resources Technology Satellite (ERTS-1) was launched on July 23, 1972 into a sun-synchronous polar orbit 914 kilometers (492 nautical miles) above sea-level. This orbit allows the satellite to circle the earth every 103 minutes and to give complete coverage of its surface every 18 days at the same time of day and with the same lighting. It is this periodic observation that gives ERTS capability for monitoring time-dependent changes in earth features.

ERTS is part of a National Aeronautics and Space Administration (NASA) program designed to demonstrate the feasibility of using earth-orbiting satellites for monitoring natural resources. ERTS collects data two ways. One is a data collection system that relays telemetered information from about 100 ground collection stations in remote areas of North America to data processing centers. The other, and key data collection capability of ERTS, involves two imaging systems called the Return Beam Vidicon (RBV) and the Multispectral Scanner (MSS) that photograph the earth in the visible and near-infrared spectrum. Because the RBV camera functioned only briefly early in the mission, the MSS has been the principal data collection system, producing tens of thousands of scenes since its launch.

The MSS simultaneously senses in 4 discrete bands (channels) covering the visible to near-infrared spectrum (designated Bands 4-7). Band 4 encompasses the 500-600 nm band (blue); Band 5, the 600-700 nm band (green); Band 6, the 700-800 nm band (red); and Band 7, the 800-1,000 nm (infra-red). It produces a continuous strip photograph of the ground below the satellite (about 185 km or 100 nautical miles square) transmitted as electronic signals to ground stations where the original channels are replicated and digitally recorded.

Data from the MSS is available either in the form of computer compatible tapes or as photographic images. The images are produced as 70 mm black and white positive transparencies (scale 1:3,359,000) for each channel. These

can be obtained separately, composited, and/or enlarged, as black and white positive or as false color transparencies and prints. They are commonly available at a scale of 1:1,000,000.

An example of a false color composite of an ERTS scene is shown on the cover of this issue of the Bulletin. An annotated black and white diagram of the same area is shown in Figure 1 and 2. This scene, imaged on October 21, 1972, at approximately 10:00 a. m., covers a 10,000 square (nautical) mile area of southern California centered on Los Angeles. This vast mountain-and-sea-girt metropolis, covering 1,500 square miles and inhabited by 8,500,000 people, is encompassed in a single scene.

One basic feature of ERTS photography is its multi-spectrality, a feature that permits identification of earth features based on their reflectance characteristics in different portions of the spectrum. Each channel or band can be analyzed as one color dimension, separately, or in several dimensions as a composited, "false color" image. The "redness" of the cover image is an example of false color representation, a result of the use of the infra-red band which penetrates haze and gives better information for vegetation. On the October image, shades of red correspond with various species of vegetation, their vigor or condition, their presence as well as near-absence (a large burned area is indicated on Fig. 2). Open spaces of the class of parks, golf courses, and cemeteries appear as bright pink areas. Cultivated crops such as irrigated alfalfa are among the brightest red colors. Commercial and industrial areas are thus recognized by the absence of red and by the presence of blue-green colors which represent man-made materials. Dark objects in the visible spectrum also appear dark in false color. Consequently, nonreflective objects such as the ocean and large areas of asphalt ap-

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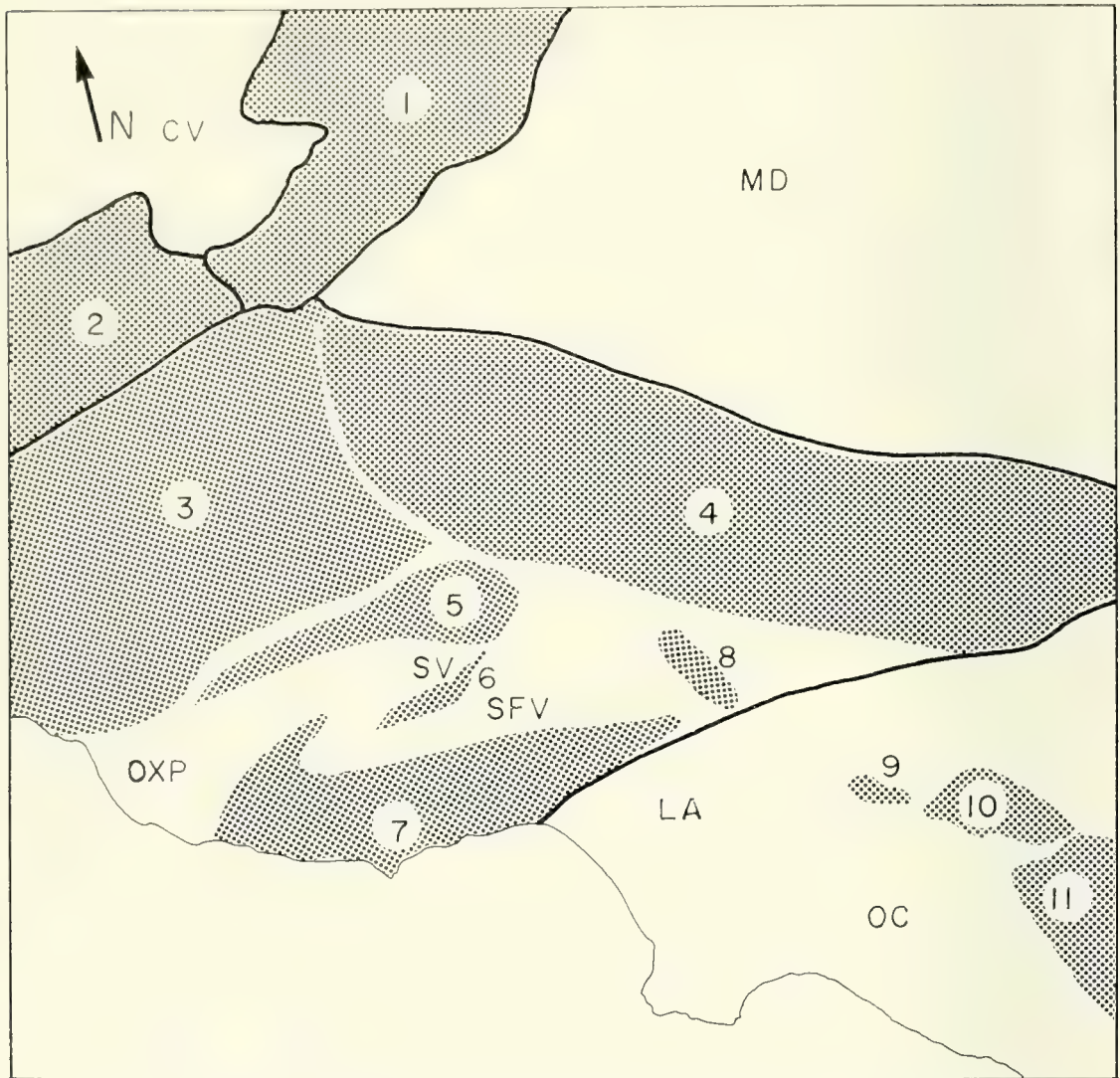


Figure 1. Guide to the mountain ranges, geomorphic provinces, and other points of interest of southern California (refer to cover illustration). 1, Sierra Nevada and Tehachapi Mountains; 2, Mt. Pinos-Tecuya Mountain—Plieto Hills area; 3, Santa Ynez Mountains; 4, San Gabriel Mountains; 5, Santa Susana Mountains and Oak Ridge; 6, Simi Hills; 7, Santa Monica Mountains; 8, Verdugo Mountains and San Rafael Hills (3-8, Transverse Range); 9, Fullerton Hills; 10, Puente Mountains; 11, Santa Ana Mountains (9-11, Peninsular Ranges). CV, Central Valley (San Joaquin Valley), note farmland; LA, Metropolitan Los Angeles; MD, Mojave Desert; OC, Orange County; OXP, Oxnard Plains; note farmland; SFV, San Fernando Valley; SV, Simi Valley.

pear black. Concrete appears light grey. Intensity of reflectance in each spectral band as well as color composition serve as indicators of ground cover and its condition. High and low quality residential areas can frequently be distinguished by the intensity of the red "signature" mixed with colors that represent streets and buildings. Tech-

niques are available to enhance particular levels in intensity in each band to facilitate identification, as well as to automatically scan, identify and measure color composition and intensity levels in the total scene. Multi-spectrality clearly is a boon to the photointerpreter.

Traditional photo-interpretative tools are widely

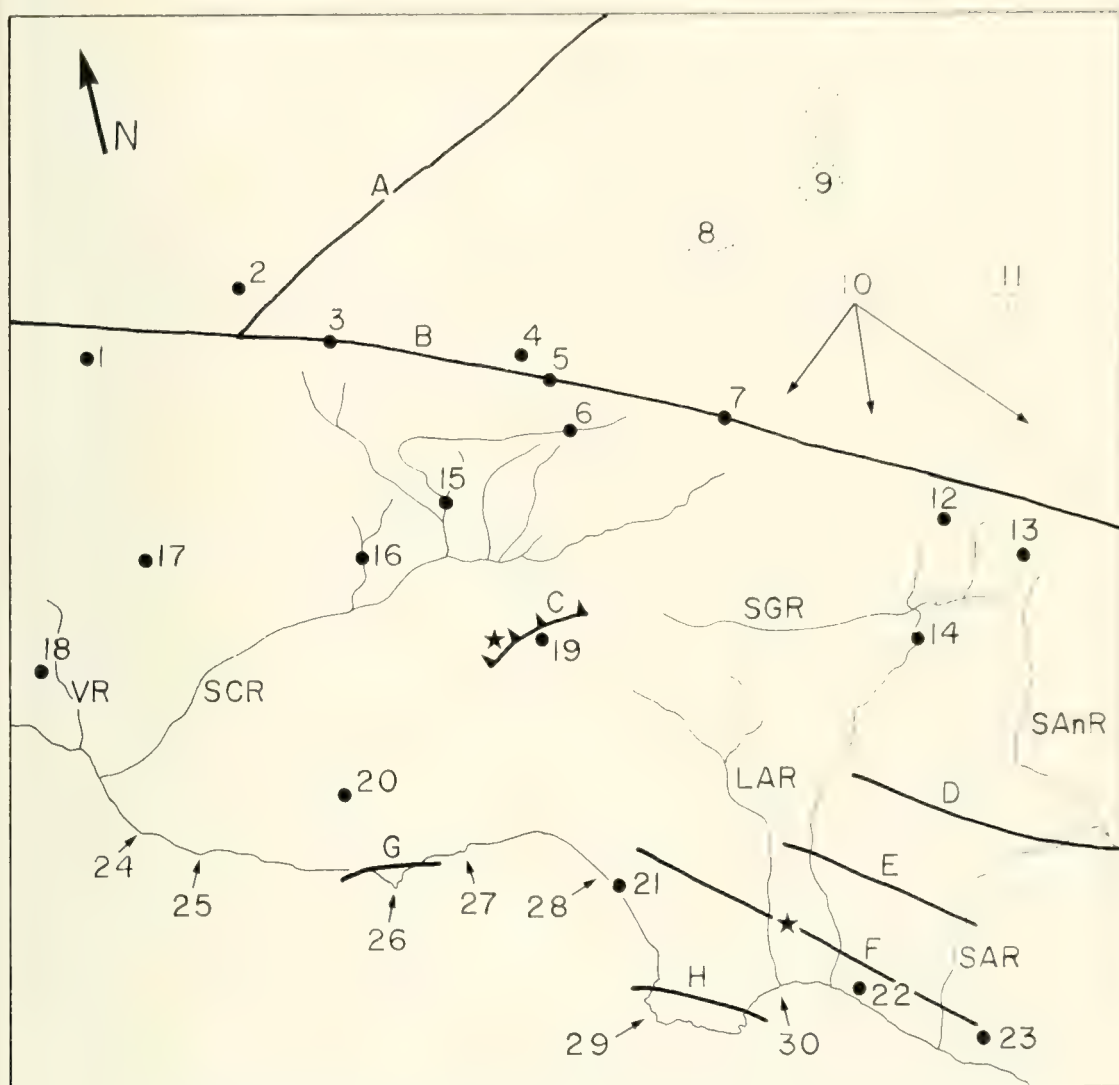


Figure 2. Guide to other points of interest shown in cover illustration. 1, Mt. Pinos; 2, Old Fort Tejon; 3, Castaic Lake; 4, Fairmont Reservoir; 5, Hughes and Elizabeth Lakes; 6, Bouquet Reservoir; 7, Lake Palmdale; 8, Rosamond Dry Lake; 9, Rogers Dry Lake; 10, alluvial fans; 11, Mirage Dry Lake; 12, Mt. Baden Powell; 13, Mt. San Antonio—"Mt. Baldy"; 14, Morris Reservoir; 15, Castaic Reservoir; 16, Lake Piru; 17, Forestfire scar; 18, Lake Casitas; 19, Van Norman Reservoir; 20, Lake Sherwood in Hidden Valley; 21, Los Angeles International Airport; 22, Anaheim Back Bay; 23, Newport Back Bay; 24, Pt. Hueneme; 25, Pt. Mugu; 26, Pt. Dume; 27, Malibu Point, note bulldozer-cleared area for Pepperdine University left of point; 28, Marina del Rey; 29, Palos Verdes Peninsula; 30, Los Angeles-Long Beach Harbor. Major faults shown in photo are: A, Garlock fault; B, San Andreas fault; C, San Gabriel fault (star indicates epicenter of 1971 Sylmar earthquake); D, Chino-Elsinore fault; E, Norwalk fault; F, Newport-Inglewood fault (star indicates epicenter of 1933 Long Beach earthquake); G, Malibu fault; H, Anacapa fault. Major river drainages shown are: LAR, Los Angeles River; SAR, Santa Ana River; SAnR, San Antonio River; SCR, Santa Clara River; SGR, San Gabriel River, VR, Ventura River.

used to interpret ERTS images. Using these tools, the more primary geomorphic and geologic features can easily be identified. Surrounding the metropolis are two great mountain systems (Fig. 1), the Transverse Mountain Ranges on its north and northwest sides and the Peninsular Ranges on its southeast side. Components of this system include the rugged San Gabriel Mountains with peaks up to 10,000 ft which wall in the northern edge of the metropolis; the Santa Monica Mountains which thrust boldly into the heart of the great city; and the Santa Ana Mountains which frame the portion of the metropolis lying in Orange County. Along the coastline, Pt. Dume and Palos Verdes are prominent headlands framing Santa Monica Bay.

Most prominent among the geologic features are the major faults: The San Andreas, the Garlock, San Gabriel, and Big Pine Faults. These faults hint at the powerful natural forces that menace the metropolis to the south. Between the San Andreas and Garlock Faults lies the broad, angular expanse of the western Mojave Desert (Antelope Valley) only 35 miles northerly of downtown Los Angeles, where many geomorphic as well as geologic features can be discerned. Among them are a series of alluvial fans, and the Rosamond and Rogers Playas (dry lake beds).

The upper left corner of the scene contains the low-lying, southern end of California's Central Valley. Dividing it from the elevated western end of the Mojave are the Southern Sierra Nevada and the Tehachapi Mountains.

Hydrologic features are clearly shown, from major rivers down to many smaller streams and tributaries. Among the major features the Los Angeles, San Gabriel, Santa Ana, and Santa Clara Rivers are identified. Other hydrologic features of note include the Los Angeles Aqueduct and a number of major reservoirs.

Agricultural districts stand out boldly. Clockwise from the top several are visible: the double-lobed irrigated district of the Antelope Valley, the dairy region in San Bernardino-Riverside Counties, the Irvine Ranch, the diverse, richly productive fields of the Oxnard Plain, and the southern San Joaquin Valley, California's largest and most important agricultural region.

The actual and potential applications of ERTS data are immense. The applications in education towards creating an awareness of the nature of

the earth's surface, its environmental character, and man's use of it are obvious. Another powerful application is in the area of scientific research involving fields such as geology, oceanography, hydrology, botany, pedology, climatology, and geography. A vast range of resource management investigations are currently under way in agriculture, forestry, fisheries, mineral exploration, and water and air quality where a wide range of analysis and data handling procedures including monitoring capabilities are being explored.

Also under study is the use of ERTS data for urban and regional planning and management. One such project, funded by NASA, is a joint study by the Regional Planning Commission of Los Angeles County, California, and the General Electric Company of Philadelphia, Pennsylvania, to evaluate ERTS-1 data for its urban and regional planning application. This project stresses a semi-automatic electronic analysis of multi-spectral information from ERTS. Results from this project indicate that ERTS-1 imagery will primarily yield new and unconventional data about the intensity of urban development, an often-used surrogate for environmental quality. Through ERTS synoptic coverage, design concepts can be defined and intra-urban as well as inter-urban comparisons made. These results stem from viewing ERTS as a new research tool, the smallest scale available in a multi-stage process of urban and regional analysis, and viewing multi-spectral analysis as a means of rapidly obtaining and identifying information for object classes that are characterized by color. These results will not replace older forms of data used by planners nor readily conform to them, but will give planners the capability to undertake old and new problems more effectively.

ACKNOWLEDGMENT

This paper is based on data obtained from the Regional Planning Commission of the County of Los Angeles, California, and the General Electric Company who are engaged in a joint project to analyze Earth Resources Technology Satellite (ERTS-1) data for its urban and regional planning applications. The joint project is completely funded by a National Aeronautics and Space Administration Grant. James Smith and Susan Payne prepared figures 1 and 2.

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LATITUDE AND LITTER SIZE OF THE CALIFORNIA GROUND SQUIRREL, *SPERMOPHILUS BEECHEYI*

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ABSTRACT: An inverse relationship between latitude and litter size was found to exist in the California ground squirrel (*Spermophilus beecheyi*). Correlation analysis of litter size with climatic and physical factors revealed that the best correlation existed between litter size and the length of the freeze-free period. It is hypothesized that the larger litter sizes in southern localities may be a response to heavier predation brought about by an opportunity for more ground squirrel activity outside the burrow at southern latitudes, where the freeze-free period is longer.

The purpose of this paper is to report on the relationship between latitude and litter size of the California ground squirrel (*Spermophilus beecheyi*) and to suggest possible reasons for the relationships which exist.

Lord (1960) reported a direct correlation between latitude and mean litter size in several "nonhibernating prey species" of mammals. Other workers have reported similar relationships for additional mammals (Rowan and Keith, 1956; Burns and Burns, 1957; Blus, 1966). Lord (1960) suggested that mortality rates for populations of these species were higher in northern latitudes than in southern latitudes, and that higher productivity was essential to offset the higher mortality rates. Because of the shorter breeding season at higher latitudes, increased productivity was accomplished through an increase in the litter size rather than an increase in the number of litters. Spencer and Steinhoff (1968) rejected Lord's hypothesis that increased litter size was a response to higher mortality rates. They proposed that "length of season and parental mortality related to reproduction" were selective forces by which mean litter size was established in the different environmental conditions encountered at the various latitudes.

Lord (1960) failed to find a significant relationship between latitude and mean litter size in the one group of "hibernating prey species" of mammals (*Spermophilus*) which he examined. He postulated that the lack of relationship between latitude and mean litter size among this group was caused by responses to the densities of breeding populations, which were related to the length of time that pressures of predation were avoided through hibernation. Spencer and

Steinhoff (1968) suggested that their hypothesis would explain the absence of latitudinal variation in litter size in ground squirrels, because these species usually have a single litter annually. Thus, the length of the breeding season would have little effect on the annual production in these species.

METHODS

During June–August, 1967–68, California ground squirrels were collected in Benton and Douglas Counties, Oregon. Adult females were examined by necropsy and implantation sites in each uterus counted. Mean numbers of implantation sites per parous female were considerably lower (Table 1) than litter sizes reported for the species in general references on mammals (Hall and Kelson, 1959; Asdell, 1964). Because of these differences, a search was conducted for information on mean numbers of embryos or implantation sites per parous female California ground squirrel. Records of litter sizes of California ground squirrels were obtained for nine other localities (Table 1). However, one of these records was not used in the correlation analysis because the mean litter size was believed to be abnormally large in response to an intensive control program (Jacobsen, 1923).

Weather data were obtained from Elford (1959) and Sternes (1960). Estimated mean altitudes of the collection sites were taken from

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state highway maps. Four climatic and physical factors were considered as possible causes of the relationship between latitude and litter size: 1) mean altitude; 2) mean annual rainfall; 3) mean annual temperature; and 4) mean length of the freeze-free period (Table 1). Statistical tests used in the analysis of the data were taken from Steel and Torrie (1960) and Dixon and Massey (1969).

RESULTS AND DISCUSSION

Mean litter sizes were plotted against corresponding latitudes, and a line was fitted to these points by the least squares method (Fig. 1). An F-test indicated that the slope of the line differed significantly from a zero slope ($P < 0.01$). The calculated coefficient of determination (0.762) implied that more than 76 percent of the variation in litter size was associated with latitude (Table 2). An inverse relationship between latitude and mean litter size in the California ground squirrel was evident. The addition of the quadratic term to the least squares line

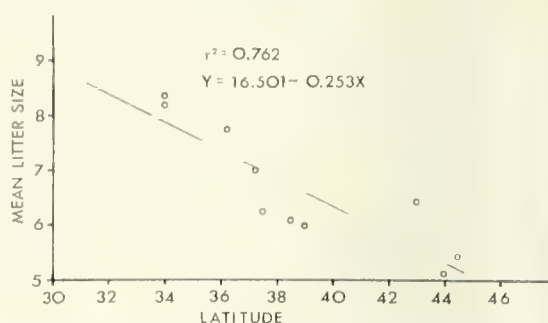


Figure 1. Relationship between latitude and mean litter size in the California ground squirrel.

plotted in figure 1 did not improve the least squares fit.

The hypothesis proposed by Spencer and Steinhoff (1968) provided explanations for both direct correlations between latitude and litter size and absence of relationships between latitude and litter size. However, their hypothesis does not appear to allow for the possibility of inverse relationships between latitude and litter size.

TABLE 1. Mean litter size, latitude, estimated mean altitude, annual rainfall, mean temperature, and mean length of the freeze-free period, for collection sites of *Spermophilus beecheyi* in California and Oregon.

Mean Litter Size	N	Latitude (North)	Estimated Mean Altitude	Mean Annual Rainfall	Estimated Mean Annual Temperature	Estimated Mean Length of Freeze-free Period	Weather ¹ Station	Source
8.36	55	34.00	1,200	14.68	61.9	325	LA Airport	Storer, 1930
8.19	4,233	34.00	1,200	14.68	61.9	325	LA Airport	U.S.P.H.S., 1926
7.75	40	36.25	2,000	13.67	57.2	275	Spreckles H.B. and Salinas	Linsdale, 1946
9.83	86	36.25	—	8.12	62.2	250	Hanford	Jacobsen, 1923
7.00	6	37.25	1,200	10.75	62.3	250	Madena	Fitch, 1948
6.25	8	37.50	1,200	14.40	59.1	275	Livermore	Evans and Holdenried, 1943
6.09	148	38.50	100	16.46	60.4	225	Davis	Tomich, 1962
6.00	47	39.00	200	15.71	61.4	200	Colusa	Tomich, 1962
6.44	9	43.00	500	33.11	53.4	225	Roseburg	This study
5.13	8	44.00	500	39.56	52.5	195	Eugene	Edge, 1931
5.46	13	44.50	200	37.67	53.0	195	OSU	This study

¹ Weather data for California were taken from Elford (1959) and weather data for Oregon were taken from Sterns (1960).

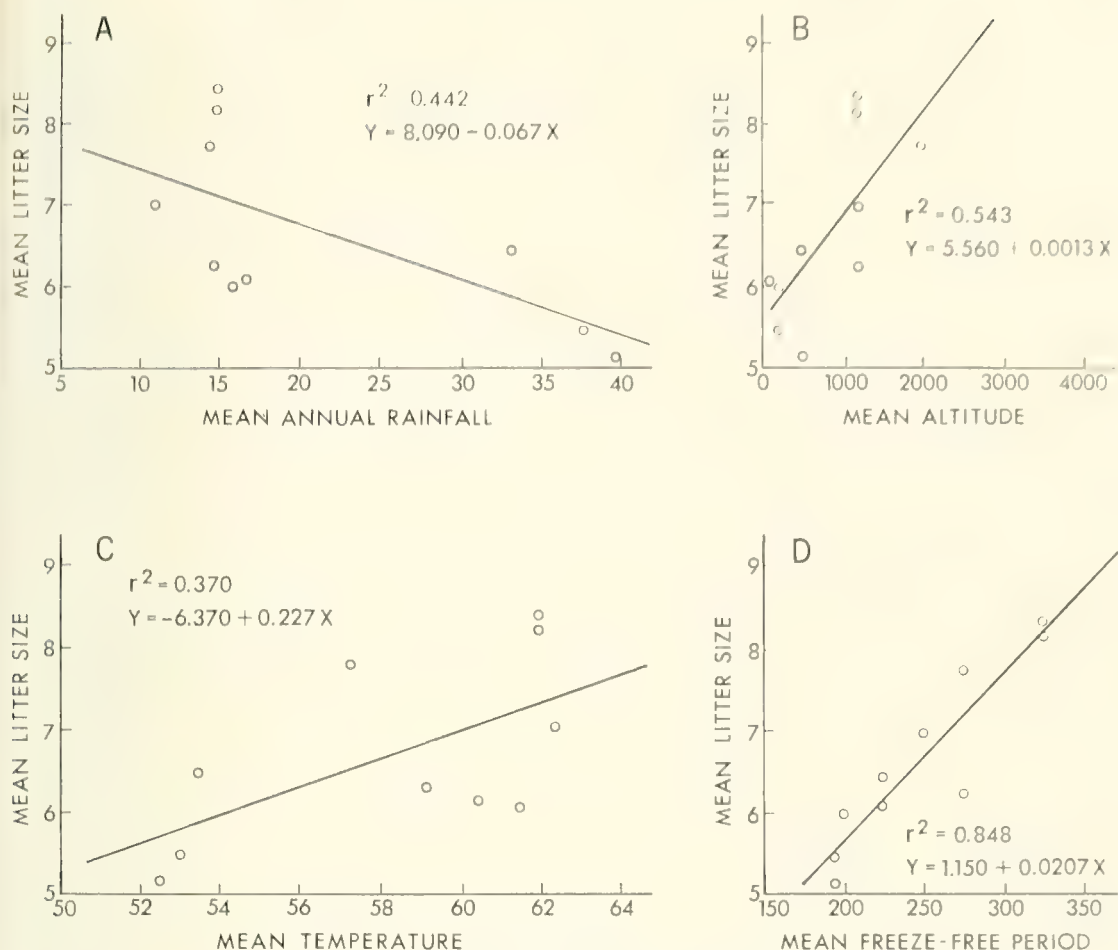


Figure 2. Correlations of litter size with climatic and physical factors. A, Mean annual rainfall (inches); B, Mean altitude (feet); C, Mean temperature (Fahrenheit); D, Mean length of the freeze-free period (days).

Differences in litter sizes of the California ground squirrel could be responses to different densities of breeding populations caused by other inimical factors related to latitude. Tomich (1962) believed that excessive rainfall was the most important adverse factor affecting populations of California ground squirrels. However, rainfall at the northern localities for which mean litter sizes were available averaged about three times that at the southern localities and the corresponding correlation (Table 2, Fig. 2A) indicated litter sizes were smaller where rainfall was heaviest.

A low level of correlation was also found when altitude was used as the independent variable (Table 2, Fig. 2B).

The correlation between litter size and mean

temperature at the various collection sites was not significant (Table 2, Fig. 2C).

Lord's (1960) hypothesis could be used to explain inverse relationships between latitude and litter size in hibernating species of mammals. This would require that the length of periods of dormancy be directly correlated with latitude, and that associated differences in rates of mortality be of sufficient magnitude to affect the observed differences in litter size. However, the California ground squirrel both hibernates and estivates (Linsdale, 1946). In southern California, Linsdale (1946) observed active ground squirrels in all months of the year, but found that adults spent as long as eight months and juveniles as long as 5½ months in their burrows

TABLE 2. Correlations of litter size of ten *Spermophilus beecheyi* with climatic and physical factors.

Correlation	r ²	s	s ²	F	Significance Level
Latitude	0.762	0.579	0.335	25.64	0.01
Altitude	0.543	0.803	0.645	9.52	0.05
Rainfall	0.442	0.887	0.787	6.34	0.05
Temperature	0.370	0.942	0.887	4.72	0.10
Freeze-free period	0.848	0.462	0.213	44.91	0.01

each year. A similar variability in periods of dormancy of *S. beecheyi* was observed in Oregon.

A possible explanation for the relationship between latitude and litter size could be the number of days suitable for ground squirrel activities outside the burrow. While we observed some ground squirrel activity in Oregon during most months, we never observed active squirrels during periods of cold or adverse weather. In order to assess this possibility, mean litter sizes were correlated with the length of the freeze-free period at each location (Table 2, Fig. 2 D). The result was an extremely high correlation indicating more than 84 percent of the variation in litter size was correlated with freeze-free period ($P < 0.01$).

We believe that the ground squirrels spend more time outside the burrows in southern latitudes and that while squirrels are active in all months of the year, the opportunity for outside activity is greater at southern locations where temperatures are warmer and consequently the opportunity for predation is correspondingly greater. Jacobsen (1923) during intensive control programs on the California ground squirrel "found that on areas where control operations had been carried on for two years or longer, thereby allowing for an increase in food supply and at the same time decreasing the numbers dependent on a certain area for food, the litters were uniformly larger than on areas where the work had either just been started this year or had been in full force for eight or nine months. While this evidence is not absolute in any way, nevertheless it would point toward an endeavor on the part of the species to come back to the larger numbers that had normally been supported on the particular piece of land."

Jacobsen's (1923) observations support our hypothesis that the larger litter sizes in southern localities may be a response to heavier predation brought about by an opportunity for more ground squirrel activity outside the burrow at southern latitudes where the freeze-free period was longer.

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RESEARCH NOTES

NONGEOGRAPHIC VARIATION IN THE LONG-NOSED BAT, *CHOERONISCUS INTERMEDIUS*

The genus *Choeroniscus* (Mammalia; Phyllostomatidae) presently contains five species all of which are rare in collections. Four (*inca*, *intermedius*, *minor*, and *periosus*) occur only in northern South America, whereas *Choeroniscus godmani*, the commonest species of the genus, occurs in Mexico, Central America, and northern South America. Owing to the apparent rarity of *Choeroniscus*, no comprehensive systematic work has been undertaken on the genus (Handley, 1966); before detailed studies of geographic variation and interspecific variation are attempted, however, a better understanding of nongeographic variation in member species is needed. Therefore, when a large series of *Choeroniscus intermedius* from Trinidad became available for study, we undertook analysis of nongeographic variation within this species, the results of which are discussed below.

All statistical analyses were performed on the IBM 360-50 computer at Texas Tech University. The univariate statistical program that was used yielded standard statistics (mean, range, standard deviation, standard error of the mean, variance, and coefficient of variation) and employed single-classification analysis of variance (*F*-test, significance level .05) to test for significant differences between the means for males and females (Sokal and Rohlf, 1969). Similar analyses have been used by Genoways and Jones (1971) and Jones, Genoways, and Baker (1971) in studies of other mammalian groups. Standard external measurements that were used were those recorded on the specimen label by the preparator; cranial measurements and length of forearm were taken in the laboratory by means of dial calipers. All measurements are recorded in millimeters. All specimens available to us were adults (phalangeal epiphyses fused). They were obtained by Baker in the course of a study of karyotypic variation in bats supported by a grant (GN 29132X1) from the National Science Foundation. Laboratory phases of the study were supported by the Institute of Museum Research, Texas Tech University.

Individual variation.—For the five external measurements studied (Table 1), the range of coefficients of variation were from 2.5 (total length for males) to 25.4 (length of tail vertebrae for females). Values for females were higher than those for males for all five external measurements. Coefficients of variation were unusually high (Long 1968, 1969; Smith 1972) for length of hind foot for females and length of tail vertebrae for both sexes. The high value for the former probably resulted from differences in the method of taking this measurement by individual preparators. Variation in tail length could be related to this also, but possibly resulted from individual

variation in this structure. The tail of *Choeroniscus* is relatively short, not reaching the posterior border of the interfemoral membrane, and probably is of little structural value.

Mastoid breadth of females had the lowest coefficient of variation (1.9) for the seven cranial measurements analyzed, whereas postorbital breadth for males had the highest value (6.8). Coefficients of variation were lower for females than for males in all seven cranial measurements. Postorbital constriction was the most variable measurement in both sexes. This measurement proved to be extremely dif-

TABLE 1. External and cranial measurements for *Choeroniscus intermedius* (10 males and 26 females) from Trinidad. 1, Total length; 2, length of tail vertebrae; 3, length of hind foot; 4, length of ear; 5, length of forearm; 6, greatest length of skull; 7, condylobasal length; 8, mastoid breadth; 9, breadth of braincase; 10, postorbital constriction; 11, length of maxillary toothrow; 12, breadth across upper molars. An asterisk indicates that the sexes are significantly different at the .05 level.

Sex	Mean	(Range)	± SE	CV
1. ♂	63.1	(61.0–66.0)	± 0.50	2.5
♀	64.3	(56.0–71.0)	± 0.68	5.4
2. ♂	7.8	(6.0– 9.0)	± 0.32	12.8
♀	7.6	(4.0–11.0)	± 0.38	25.4
3. ♂	8.5	(7.5– 9.0)	± 0.18	6.8
♀	8.8	(7.0–11.0)	± 0.18	10.3
4. ♂	12.8	(11.0–14.0)	± 0.31	7.8
♀	12.1	(10.0–14.0)	± 0.22	9.3
5. ♂	34.1	(32.5–35.7)	± 0.34	3.2
♀	34.7	(26.5–38.4)	± 0.39	5.8
6. ♂ *	21.8	(21.2–22.9)	± 0.19	2.7
♀	23.1	(22.3–24.1)	± 0.10	2.1
7. ♂ *	21.2	(20.5–22.0)	± 0.17	2.5
♀	22.5	(21.6–23.4)	± 0.10	2.3
8. ♂ *	8.3	(8.0– 8.6)	± 0.07	2.6
♀	8.6	(8.4– 9.0)	± 0.03	1.9
9. ♂ *	8.3	(8.1– 8.8)	± 0.07	2.5
♀	8.5	(8.1– 8.9)	± 0.04	2.1
10. ♂	3.6	(3.3– 4.1)	± 0.08	6.8
♀	3.7	(3.3– 4.1)	± 0.05	6.4
11. ♂ *	7.5	(7.0– 7.9)	± 0.09	3.6
♀	8.1	(7.5– 8.7)	± 0.05	3.0
12. ♂	4.3	(4.0– 4.7)	± 0.07	5.2
♀	4.3	(4.2– 4.7)	± 0.03	3.5

ficult to take with dial calipers, undoubtedly resulting in the high values.

Secondary sexual variation.—Analysis of variance revealed that males were significantly different from females in five (greatest length of skull, condylobasal length, mastoid breadth, breadth of braincase, and length of maxillary toothrow) of the 12 measurements tested (Table 1). Females were larger than the males in all of these measurements. In the remaining seven, males averaged larger in two (length of tail vertebrae and length of ear) and females were larger in five (total length, length of hind foot, length of forearm, postorbital constriction, and breadth across upper molars).

Conclusions.—Of the 12 measurements analyzed, only length of tail exhibited enough individual variation to warrant its deletion in analysis of geographic or interspecific variation in the genus *Choeroniscus*. Also, because of the difficulty in consistently taking the measurement, we also suggest elimination of post-orbital constriction.

Specimens of *Choeroniscus intermedius* were found to exhibit significant secondary sexual variation in five of the 12 measurements studied. Therefore, it is clear that males and females should be separated in analyses of variation within members of the genus. Females were found to be the larger in 10 of the 12 measurements—similar to the situation found in several other groups of bats (see for example, Jones and Schwartz, 1967; Jones *et al.*, 1971; Peterson, 1965).

Specimens examined.—TRINIDAD: Blanchisseuse, 5; Guayaguayare, 12; Las Cuevas, 14; Maracas Valley, 1; San Rafael, 4.

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A NEW SPECIES OF *ELEUTHERODACTYLUS* (AMPHIBIA: LEPTODACTYLIDAE) FROM ANDEAN ECUADOR

Access to the Amazonian slopes of the Ecuadorian Andes has been difficult in the past except through the deep canyon of the Río Pastaza (Baños de Puyo), and this route traverses little of the altitudinal transect on the eastern face of the Cordillera Oriental. The building of the Texaco-Gulf transandean pipeline prompted the construction of a road along its course and field parties from the University of Kansas have worked the Amazonian slope portion of the transect as it was being developed. On one of his trips along this road, William E. Duellman secured two specimens of a moderate-sized frog beneath rocks in a stream. At first glance the frogs appeared to be a treefrog of the genus *Hyla*, but dissection of the digits and closer examination revealed them to represent a distinctive new species of *Eleutherodactylus*.

Eleutherodactylus pugnax, new species

Holotype.—University of Kansas Museum of Natural History (KU) 146466, an adult female collected at Salto de Agua, 2.5 km NNE Río Reventador, Napo Prov., Ecuador, 1660 m by W. E. Duellman, Bruce MacBryde, and John Simmons, 7 April 1972.

Topoparatype.—KU 146467, a male, collected syntopically.



Figure 1. Male paratype of *Eleutherodactylus pugnax*, new species. From a kodachrome by William E. Duellman.

Diagnosis.—A species of *Eleutherodactylus* unique in the following combination of characters: first finger shorter than second; all digits bearing broad discs; toes basally webbed with prominent lateral fringes; skin of venter coarsely areolate; ear absent (no tympanic annulus, cavum tympanicum, or columella); snout round in dorsal view, truncate in lateral profile, shorter than eye length; prevomerine dentigerous processes and teeth present.

Only three other species of *Eleutherodactylus* now known lack ears—*E. anotis* Walker and Test (Venezuela), *E. surdus* (Boulenger) (high Pacific slopes of Andean Ecuador), and an unnamed species from the paramos of southern Ecuador. None of these has toe webbing or the prominent lateral fringes of the toes seen in *E. pugnax*. All three also have longer snouts (eye length equal to or less than eye-nostril distance). The unnamed species is a small frog (adult females 20–21 mm SVL) with minute prevomerine processes and concealed prevomerine teeth.

Description.—Head as wide as body, wider than long; snout semicircular in dorsal outline, truncate in lateral profile (Fig. 1), short, eye length much greater than eye-nostril distance; upper jaw barely overhanging lower jaw; canthus rostralis round, concave; nostrils near tip of snout, protuberant, directed laterally; loreal region flat; lips not flared; eyelids narrow, their width about equal to interorbital distance; interorbital space flat, no frontoparietal ridges; frontoparietals complete, no fontanelle, not in contact with nasals; nasals narrowly separated; supratympanic fold thick, glandular; tympanum absent;



Figure 2. Left, foot of holotype of *Eleutherodactylus pugnax*. Right, hand of holotype of *Eleutherodactylus pugnax*.

tongue longer than wide, weakly notched posteriorly, posterior edge free; choanae round, slightly larger than a prevomerine dentigerous process, not concealed by palatal shelf of maxillae; prevomerine dentigerous processes round, median and posterior to choanae, bearing 3–4 teeth along the posterior border.

Skin of dorsum bearing flattened, ill-defined warts; flanks areolate; skin of upper eyelid covered with numerous wart-like ridges; skin of venter and about anus coarsely areolate; discoidal folds prominent; concealed surfaces of limbs smooth; upper surfaces of limbs smooth with scattered flattened warts; outer edge of forearm bearing a row of ulnar warts; three palmer tubercles, inner largest; numerous well-defined supernumerary palmer tubercles; subarticular tubercles round, non-conical, distal tubercles tend to be bifid; fingers bearing weak lateral fringes, lacking web (Fig. 2); all digits bearing discs which are wider than long; discs largest on fingers II, III, and IV; first finger shorter than second.

No tubercles on heel or outer edge of tarsus; inner edge of tarsus bearing a fold along its distal one-third; two metatarsal tubercles, outer flat, ill-defined, one-fifth to one-sixth size of elongate inner (twice as long as wide, not compressed); few supernumerary plantar tubercles; subarticular tubercles smaller than those of fingers, elongate, simple, non-conical; toes bearing discs that are smaller than those of fingers; toes with prominent lateral fringes (Fig.

2) and basal webbing; the webbing formula for the holotype (based on the formula given by Savage and Heyer, *Beit. Neotropischen Fauna* 5:111-131, 1968): I 2'-2 II 2'-3' III 2½-4' IV 3¼-2½ V; legs of moderate length, heel of adpressed hindlimb reaches to tip of snout; when legs are flexed at right angles to the sagittal line, heels touch.

The holotype is an adult female with convoluted oviducts and a few moderate-sized (2.0 mm in diameter) yellow eggs interspersed among many small (0.5-1.0 mm) white eggs. The paratype is an adult male with vocal slits and a sub-gular vocal sac; the testes are large and white and the thumbs are swollen at their bases. The measurements (in mm) are as follows; data for the holotype are given first, data for the paratype follow in parentheses: snout-vent length 30.8 (22.1), shank 17.0 (12.2), head width 12.2 (8.6), head length 9.7 (7.3), eyelid width 2.6 (1.7), interorbital distance 2.5 (2.2), eye length 4.2 (3.0), eye-nostril distance 2.8 (2.5).

In preservative, *E. pugnax* is brown with darker brown blotches, interorbital triangle, and limb bars. The limb bars are about as wide as the interspaces. Dark brown canthal and supratympanic stripes and labial bars are present. The posterior surfaces of the thighs are brown with cream flecks. The venter of the female is dirty cream with numerous brown spots; the lower surfaces of the hindlimbs are brown with cream reticulation. The venter of the male is creamy-white with a few brown flecks (primarily on the lower venter); the undersides of the thighs are heavily speckled with brown.

In life, *E. pugnax* was described as "Dorsal surfaces and flanks grayish-brown with dark brown markings. Venter gray with brown flecks. Iris reddish-brown." (W. E. Duellman field notes, 7 April 1972).

Etymology.—Latin, *pugnax*, meaning fighter; in loose reference to the collector, William E. Duellman.

Natural history.—The pronounced lateral fringing and basal webbing of the toes suggests that *E. pugnax* is a riparian species. The holotype and paratype were collected beneath rocks in a fast-moving stream in cloud forests by day. The male is reproductively active (swollen, non-spinous thumb; large testes) but the female probably is not.

Relationships.—Few mainland *Eleutherodactylus* species have toe webbing; those that do (e.g., *E. anomalus*, *E. bufoniformis*, *E. fitzingeri*) are members of the *E. binotatus* group [first finger longer than second, skin of venter smooth, ear prominent (i.e., tympanic annulus large and externally visible)] and frequently live near streams. The West Indian *Eleutherodactylus* with toe webbing and prominent fringes are likewise strongly riparian in habit (Schwartz, *Stud. Fauna Curacao and other Carib. Islands* 24:1-62; Shreve and Williams, in Williams, *et al.*, *Bull. Mus. Comp. Zool.* 129:291-342, 1963). I do not think that either of the more distinctive

features of *E. pugnax* (earlessness, toe webbing) are reliable indicators of relationship.

Eleutherodactylus pugnax is a member of the Cochran and Goin's (Bull. United States Nat. Mus. (288):1-655, 1970) Group II which I prefer to call the *E. unistrigatus* group, defined by having a granulate or areolate skin on the venter and the first finger being shorter than the second. *Eleutherodactylus pugnax* has no apparent close relatives within this group.

William E. Duellman loaned the specimens, provided additional information about the locality and its habitat, and permitted me to use his kodachrome of the frog.

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A NEW SPECIES OF TREMATODE (TREMATODA: MONOGENEA) FROM THE GILLS OF *DIAPHUS WATASEI* JORDAN AND STARKS, 1904.

Through the courtesy of B. Nafpaktitis, Department of Biological Sciences, University of Southern California, some monogenetic trematodes from the gills of a myctophid fish, *Diaphus watasei* Jordan and Starks, 1904 (identified by Nafpaktitis) were obtained for study. The fish were collected between 400 and 450 fathoms off the southeast coast of Africa by the Anton Brunn International Indian Ocean Expedition. Two of eighteen fish had a total of five parasites that are described here as a new species of *Diclidophora* Diesing, 1850. They were stained with Mayer's paracarmine, cleared with methyl benzoate, and mounted in Canada balsam. Measurements are expressed in microns.

Diclidophora sprostonae, new species

Diagnosis: With the characters of the genus. Length 2198, 1092 wide. Opisthaptor attached to ventral side of body, with 8 short peduncles and clamps (two lost from best extended specimen) 770 long, 182-266 wide. Clamps with muscular pads, 140-160 long, 112-126 wide. Body tapers anteriorly. Oral cavity followed by pharynx 65 long, 44 wide. Esophagus 2-3 times length of pharynx. Intestinal crura confluent posteriorly with numerous diverticula directed peripherally and medially. A diverticulum extends into opisthaptor. Testes arranged in radiating cords, mainly postovarial between intestinal crura. Convoluted vas deferens extends anteriorly to ventral genital pore at mid-esophageal

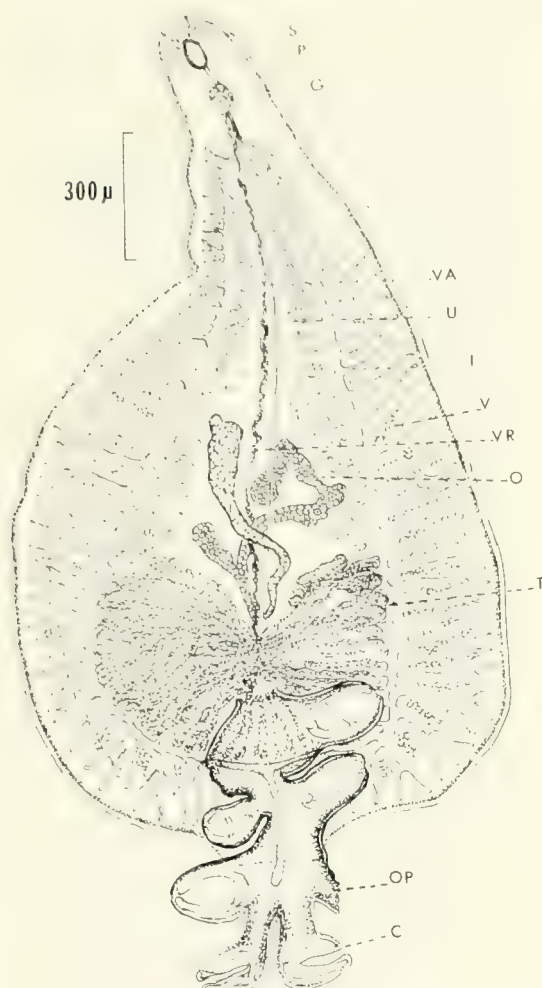


Figure 1. Ventral view of *Diclidophora sprostonae*, new species; C, clamps; G, genital pore; I, intestine; O, ovary; OP, opisthaptor; P, pharynx; S, sucker; T, testes; U, uterus; V, vitellaria; VA, vas deferens; VR, vitelline reservoir.

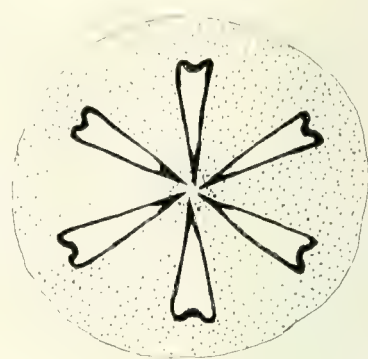
level. Cirrus diameter about 30, armed with six curved spines about 9 long, ovary ribbon-like, looped, median and pretesticular. Vitelline follicles small, numerous, in groups between intestinal diverticula and extending into opisthaptor. Vitelline reservoir adjacent to ovary, with expanded anterior end. Genitointestinal canal on right side. Seminal receptacle not seen. Uterus median, tubular, from testicular level to common genital pore. None contained eggs.

Host: *Diaphus watasei* Jordan and Starks, 1904.

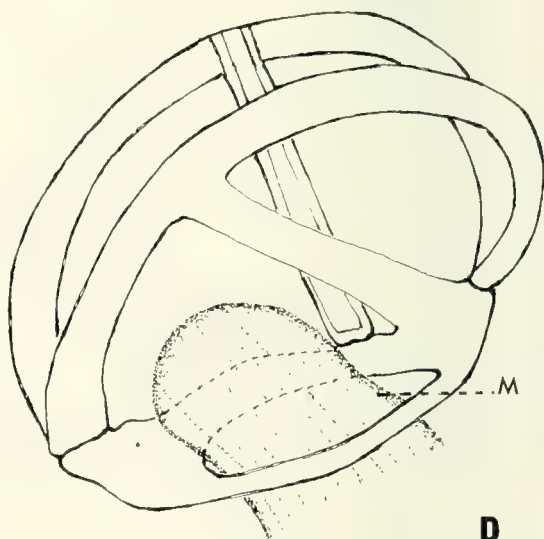
Habitat: Gills.

Type Locality: Off southeast coast of Africa.

Holotype: No. 639, deposited in the Hancock Parasitology Collection, University of Southern California.



A



B

Figure 2. A, Cirrus spines and B, sclerites of clamp; (M, muscular pad) of *Diclidophora sprostonae*, new species.

DISCUSSION

These worms were removed from the gills of fish that had been preserved for several years and most of them were poorly distended. *Diclidophora sprostonae* differs from other species of the genus in the numbers of cirrus spines and in the fan-like arrangement of the testes. Several authors (Llewellyn and Tully, J. Fish. Res. Bd. Canada, 26: 1063-1074, 1969; Sproston, Trans. Zool. Soc. London, 25: 185-600, 1946, etc.) have mentioned the variation in the number of cirrus spines or hooks in individuals of the same species. All specimens of *Diclidophora sprostonae* possess six hooks. Perhaps a larger number of specimens might show variation in this character. Although all specimens

appeared mature, none had eggs. Yamaguti (Systema Helminthum, Vol. IV. Monogenea and Aspidocotylea. Intersci. Publ., New York, 1963) stated that members of the genus *Diclidophora* are parasitic on the fish families Gadidae, Merlucciidae, and Macrouridae. The present paper adds the family Myctophidae. Monogenetic trematodes are generally considered to be host specific.

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A NEW SPECIES OF *STRAPAROLLUS* (ARCHAEOGASTROPODA) FROM THE MISSISSIPPIAN OF NEVADA

During a recent biostratigraphic study (Mount, 1972a, 1972b) of the larger invertebrates in the Upper Paleozoic section of the central Pancake Range, Nye County, Nevada, I placed particular emphasis on the distribution of Mollusca in the Mississippian and Pennsylvanian rocks. Excluding the Cephalopoda, mollusks of this age are poorly known in the Great Basin area of North America. In his pioneering study of the Eureka district of Nevada, Walcott (1884) described several new bivalves and gastropods, however in later years so little attention has been given to this group that at the present time it is virtually useless for age determination and correlation. Recently, the stratigraphic positions of Walcott's species have become better known as a result of the biostratigraphic work of Gordon (1971). It is the purpose of this paper to describe a new species of the gastropod *Straparollus*. Numerous fossil lists include reference to this genus, but it is generally represented by material too poorly preserved or too scanty to allow species assignment. References to the Department of Geological Sciences, University of California, Riverside, are hereafter abbreviated as UCR.

Family Euomphalidae de Koninck, 1881

Genus *Straparollus* de Montfort, 1810

Subgenus *Euomphalus* Sowerby, 1812

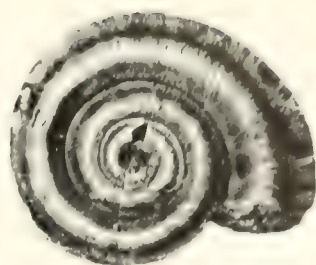
Straparollus (*Euomphalus*) *pancakensis*, new species

Figure 1

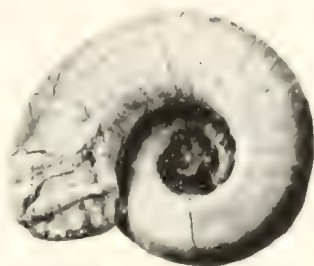
Straparollus (*Euomphalus*) n. sp. A: Mount, 1972b, p. 75, pl. 2, figs. 18, 19, 20.

Diagnosis: Shell relatively small; whorls 5; spire slightly elevated; single high, broad, rounded spiral rib medially situated between the upper suture and outer shoulder.

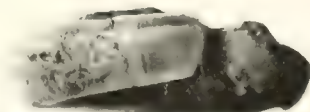
Description: Shell relatively small for the genus, subdiscoidal; spire slightly elevated, the first two



A



B



C

Figure 1. *Straparollus* (*Euomphalus*) *pancakensis*, new species. Holotype UCR 7101/1. A. Top view. B. Basal view. C. Apertural view. $\times 2$.

whorls flattened; moderately phaneromphalus, umbilicus deep with nearly vertical sides, umbilical angle near 80 degrees. Whorls 5, with moderately rounded angulations on outer-upper and -lower shoulders, outer sides of whorl moderately convex, umbilical profile of whorl weakly convex to flattened. Upper sutures shallow and slightly impressed, passing around the previous whorl just below the upper shoulder. Protoconch unknown. Spiral sculpture consists of a single high, broad, rounded rib between upper suture and angulation on the outer shoulder, width of rib about one third that of whorl, slopes of rib slightly concave. Growth lines orthocline, extending outward to rib on upper whorl, there bending into a sharply defined but shallow sinus; beyond the growth lines curve slightly backward around whorl to lower suture forming a slightly projecting upper lip over the aperture.

Holotype: UCR 7101/1; height 7.8 mm, diameter 20.8 mm, height of aperture 6.0 mm.

Paratypes: UCR 7101/2; height 7.3 mm, diameter 20.5 mm, height of aperture 6.7 mm (shell incomplete). UCR 7101/3; height 5.2 mm, diameter 18.8 mm, height of aperture 4.1 mm (shell incomplete).

Type locality: UCR locality 7101; 6530 feet south and 675 feet west of long. 115° 50' W., lat. 38° 55' N.; at elevation of 7,240 feet on crest of ridge extending west from first hill north of hill 7865, Brown Summit 7½ minute quadrangle (1968 edition), Nye County, Nevada (same as Department of Geology, University of California, Los Angeles, locality 6058-60).

Stratigraphic Position: Ely Group, Moleen Formation, unit 60 of Mount (1972a, 1972b); the fossils occur in platy, thin-bedded, dark gray, silty limestone 20 feet above the base of the formation and can be collected best from the abundant weathered platy slabs that cover the slopes.

Age: In addition to the gastropod described here, the following fossils have been identified:

SCYPHOZOA: *Paraconularia* sp.

BRACHIOPODA: *Composita* cf. *C. subquadrata* Hall, *Leiorhynchus carboniferum* Girty, *Ovatia* sp. indet.

GASTROPODA: *Bellerophon* (*Bellerophon*) sp.

BIVALVIA: *Aviculopecten* cf. *A. affinis* Walcott, *Aviculopinna* cf. *A. consimilis* (Walcott), *Schizodus* cf. *S. semistriatus* Girty.

SCAPHOPODA: *Plagioglypta* sp. indet.

TRILOBITA: *Paladin* sp.

BLASTOIDEA: *Pentremites* sp. indet.

CONODONTA: *Cavusgnathus gigantus* Gunnell, *C. lautus* Gunnell, *C. spathus* Dunn, *Gnathodus* aff. *G. girtyi simplex* Dunn, *G. muricatus* (Dunn), *Spathognathodus* cf. *S. minutus* (Ellison), *Streptognathodus unicornis* Rexroad and Burton.

This fauna is judged to be Late Chester (Late Mississippian) in age and is assigned to the upper part of the *Rhipidomella nevadensis* Assemblage Zone of Sadlick (1954). This assignment is based primarily on the presence of the conodont *Gnathodus* aff. *G. girtyi simplex* which occurs in this zone in southern Nevada (Webster, 1969) and of the characteristic Mississippian brachiopods *Composita* cf. *C. subquadrata* and *Leiorhynchus carboniferum*. Also, about 175 feet higher in the same section *Rhipidomella nevadensis* (Meek) is abundant in beds that also contain Mississippian species of the brachiopod genera *Anthracospirifer*, *Cleiothyridina*, *Flexaria*, *Inflatia*, and the bryozoan *Archimedes*.

Discussion: *Straparollus* (*Euomphalus*) *pancakeensis* is easily distinguished from all other species of the subgenus *Euomphalus* by its more strongly pronounced revolving rib which is more medially located between the upper suture and outer shoulder. The only North American species that approaches it is *S. (E.) umbilicatus* (Meek and Worthen, 1860: 462) from the Middle Pennsylvanian Desmoines

Series of Illinois (Knight, 1934: 151), the latter form having a much higher spire, larger number of whorls, narrower spiral rib, and more angulated whorl profile.

Straparollus (*Euomphalus*) *planodorsatus* (Meek and Worthen, 1860: 462) from the Mississippi Valley is the only species of this subgenus recorded from the Chester Series and it is readily distinguished from the new form described here by the lack of a spiral rib, more rounded whorl profile, higher spire, and somewhat larger size.

The new name proposed here refers to the Pancake Range, the type locality.

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A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, method, results, discussion, and conclusions, acknowledgments, and literature cited. Avoid using more than two levels of subheadings.

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Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. Omit periods after standard abbreviations: 1.2 mm, 2 mi, 30 cm, but Figs. 1-2. Use numerals before units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedure as outlined in the International Code of Botanical Nomenclature (Lawson *et al.*, 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan *et al.*, 1958), and the International Code of Zoological Nomenclature (Stoll *et al.*, 1961). Special attention should be given to the description of new taxa, designation of holotype, etc.

The literature cited section should include six or more references; entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452-458.

Brattstrom, B. H. 1969. The condor in California. Pp. 369-382 in Vertebrates of California. (S. E.

Payne, ed.), Univ. California Press, xii + 635 pp.

If fewer than six references are cited they should be inserted in text as follows:

(McWilliams, Insect mimicry, p. 216, 1970); (Holmes and Speak, J. Mamm., 54: 452-458, 1971); (Brattstrom, The Condor in California, Pp. 369-382, in Vertebrates of California, 1969).

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BULLETIN OF THE SOUTHERN CALIFORNIA
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ON THE STATUS OF *PAGURUS MERTENSII* BRANDT, WITH DESCRIPTIONS OF A
NEW GENUS AND TWO NEW SPECIES FROM CALIFORNIA
(CRUSTACEA: DECAPODA: PAGURIDAE)

PATSY A. McLAUGHLIN¹ AND JANET HAIG²

ABSTRACT: The discovery of a hermit crab identifiable with *Pagurus mertensii* Brandt [*sensu stricto*] has precipitated a review of the status of this species and its relationship to *Parapagurus mertensii* Holmes. As a result, *Pagurus mertensii* Brandt is reinstated as a distinct species and a new genus is established for the species assigned, by Holmes, to *Parapagurus* and for an additional new species from California.

Brandt (1851) described *Pagurus mertensii*, relating it to the North American species, *Pagurus splendescens* Owen. In his brief description, Brandt merely listed those characters which would distinguish *P. mertensii* from the latter species. Although the type locality was indicated by Brandt as Kamchatka, he also reported this species from California and Alaska.

Benedict (1892) placed *P. mertensii*, without description, in his subgenus *Labidochirus*, thus relating it, as Brandt had done, to *P. splendescens*. Presumably, his action was based on his misidentification of specimens from the California collections of the "Albatross" as *Eupagurus mertensii* (Brandt). Subsequently, Holmes (1900) examined a female specimen of Benedict's alleged *E. mertensii*, interpreted its gill structure to be trichobranchiate, and transferred the species to the genus *Parapagurus*.

Makarov (1938, 1962), after examining the collections of the Zoological Institute of the Academy of Sciences (USSR), including the remaining specimens of Brandt's original material, concluded that *Pagurus mertensii* [*sensu* Brandt] was synonymous with *Pagurus hirsutiusculus* (Dana). Because of the obvious distinction between *P. hirsutiusculus* and Holmes' species, Makarov accepted Holmes' assignment of the California species to the genus *Parapagurus*.

The recent discovery of a specimen identifiable with *Pagurus mertensii* Brandt [*sensu stricto*] and the reexamination of the "Albatross" collections

identified by Benedict as *Eupagurus mertensii* have shown not only that *Pagurus mertensii* Brandt *s.s.* is distinct from both *P. hirsutiusculus* (Dana) and *Parapagurus mertensii* Holmes, but that the latter species is incorrectly assigned to the genus *Parapagurus*. This conclusion regarding Holmes' species was also arrived at, independently, by de Saint Laurent (1972). This species, and a second new species from the collections of the Allan Hancock Foundation, represent a new genus of the Paguridae.

The institutions providing material for this study or which will serve as depositories for the collections are abbreviated in the text as follows: Allan Hancock Foundation (AHF); British Museum (BM); Muséum National d'Histoire Naturelle (MNHN); National Museum of Natural History, Smithsonian Institution (USNM); Rijksmuseum van Natuurlijke Historie (RMNH). The abbreviation, SL, refers to the shield length of the specimens; the symbols, ♀ and ♀♀, refer to nonovigerous and ovigerous females respectively.

This paper is scientific contribution No. 1688 from the Rosenstiel School of Marine and Atmospheric Sciences and No. 346 from the Allan Hancock Foundation.

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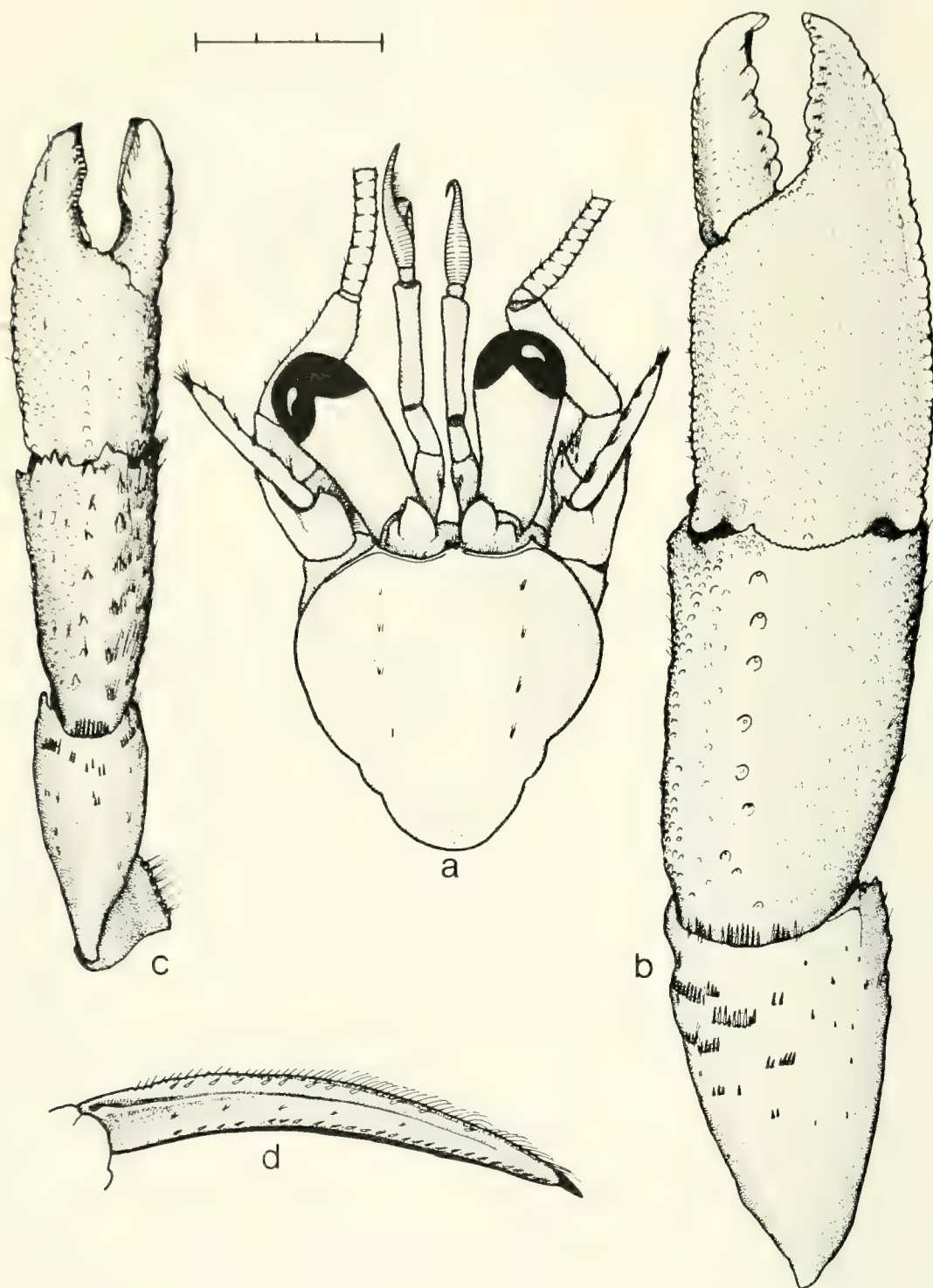


Figure 1. *Pagurus mertensii* Brandt s.s. ♂ (SL = 4.5 mm), from Pribilof Is.: a, shield; b, right cheliped (dorsal view); c, left cheliped (dorsal view); d, left P₃ dactyl (mesial view). Scale equals 3 mm (from McLaughlin, 1972).

FAMILY PAGURIDAE

Pagurus mertensii Brandt [sensu stricto]

Figures 1-3

Pagurus Mertensii Brandt, 1851 [in part], p. 112
[type locality (by implication): "Kamtschatka"].

Eupagurus mertensi: Doflein, 1900, p. 341.

Parapagurus mertensii: Alcock, 1905 [in part], p. 172.—Gordan, 1956 [in part], p. 338 (see discussion).

Pagurus mertensii: Williams, 1915, p. 477.

Pagurus hirsutiusculus: Makarov, 1938 [in part], p. 181; 1962 [in part], p. 171 (see discussion).

not *Eupagurus Mertensii*: Stimpson, 1857, p. 483; 1858, p. 237 [= *Pagurus hirsutiusculus hirsutiusculus* (Dana, 1851)].

not *Eupagurus (Labidochirus) mertensii*: Benedict, 1892, p. 2 [by implication] [= *Parapagurodes makarovi* n. sp.].

not *Eupagurus mertensi*: Lenz, 1901, p. 444 [= *Pagurus hirsutiusculus hirsutiusculus* (Dana, 1851)].

not *Eupagurus mertensii*: Stimpson, 1907, p. 216 [= *Pagurus hirsutiusculus hirsutiusculus* (Dana, 1851)].

DIAGNOSIS.—Shield longer than broad; rostrum short, obtusely rounded; ocular peduncles short, stout, with corneae noticeably dilated. Right cheliped elongate, slender; chela with dorsal surface convex, granular; carpus with dorsal surface granular, midline with irregular row of small tubercles. Left cheliped elongate, slender; chela with dorsal surface convex, granular, with short row of tubercles in midline proximally. Ambulatory legs with dactyls moderately long, broad, strongly twisted. Fourth pereopods each with strong spine at dorsodistal margin of carpus. Males with coxae of fifth pereopods symmetrical, gonopores paired, no sexual tubes. Pleopods unpaired, pl_3 to pl_6 with exopodites well developed, endopodites rudimentary.

MATERIAL EXAMINED.—1 ♂ (SL = 4.5 mm), Saint Paul I., Alaska, 1897. B. A. Stevens collection, USNM 143006.

DISTRIBUTION.—Kamchatka (Brandt); Alaska, Pribilof Islands; depth unknown.

DISCUSSION.—As previously indicated, Brandt's (1851) description of *Pagurus mertensii* consisted only of those characters which would distinguish his species from Owen's (1839) *P. splendescens*. Although Brandt implied that Kamchatka was the type locality of *P. mertensii*, he included Alaska and California in its range, on the basis of specimens collected by Wosensenski. At that time Dana's (1851) work on the collections of the United States Exploring Expedition had not been published and Brandt was unaware of Dana's description of *P. hirsu-*

tiusculus, a highly variable and superficially somewhat similar species. From the evidence presented by Makarov (1938, 1962) it would appear that Brandt confounded *P. mertensii* and *P. h. hirsutiusculus*, and that his Kamchatkan specimen is no longer extant. In a study of northwestern North American pagurids, a specimen has been found which is clearly identifiable with *P. mertensii* s.s. A complete description of this species is given by McLaughlin (in press); it is here proposed that the name *Pagurus mertensii* Brandt be restricted to the species exemplified, in part, by Brandt's (1851, p. 112) description, and by the specimen herein diagnosed and illustrated. Reexamination of the "Albatross" California collections, including those identified by Benedict as *Eupagurus mertensii* (Brandt), while confirming Makarov's conclusion that Holmes' *Parapagurus mertensii* is distinct from Brandt's species, has shown that Holmes' species is incorrectly assigned to *Parapagurus* and is herein transferred to a new genus.

As may be seen from the synonymy of *Pagurus mertensii* s.s., and the exclusions therefrom, most records of this species should be referred to *P. h. hirsutiusculus*. The records of Alcock (1905) and Gordan (1956) are merely citations from the literature and must be considered to include both *P. mertensii* s.s. and *P. h. hirsutiusculus*, as well as *Parapagurodes makarovi* n. sp.

Parapagurodes, new genus

Parapagurus: Holmes, 1900 [in part], p. 155 [not *Parapagurus* Smith, 1879].

Type Species: *Parapagurodes makarovi*, new species (see p. 119). Gender: Masculine.

DEFINITION.—Eleven pairs of phyllobranchiate gills. Third maxilliped with basis-ischium fusion incomplete; ischium with crista dentata well developed, one accessory tooth; merus and carpus each with spine at dorsodistal margin. Maxillule with proximal endite tapered; endopodite with external lobe moderately well-developed, not recurved. Ocular peduncles short or moderately short, stout, with corneae dilated. Ocular acicles slender to moderately broad, triangular or subtriangular, terminal spine submarginal. Antennular peduncles with one or two short setae on dorsodistal surface of ultimate segment. Chelipeds unequal, right larger than left. Second and third pereopods with dactyls moderately elongate, slender, not strongly twisted. Fourth pereopods subchelate or not subchelate; dactyls usually with preungual process (cf. de Saint Laurent, 1970a) on lateral face; propodal rasp weakly or moderately well-developed. Males with coxae of fifth pereopods symmetrical, right with

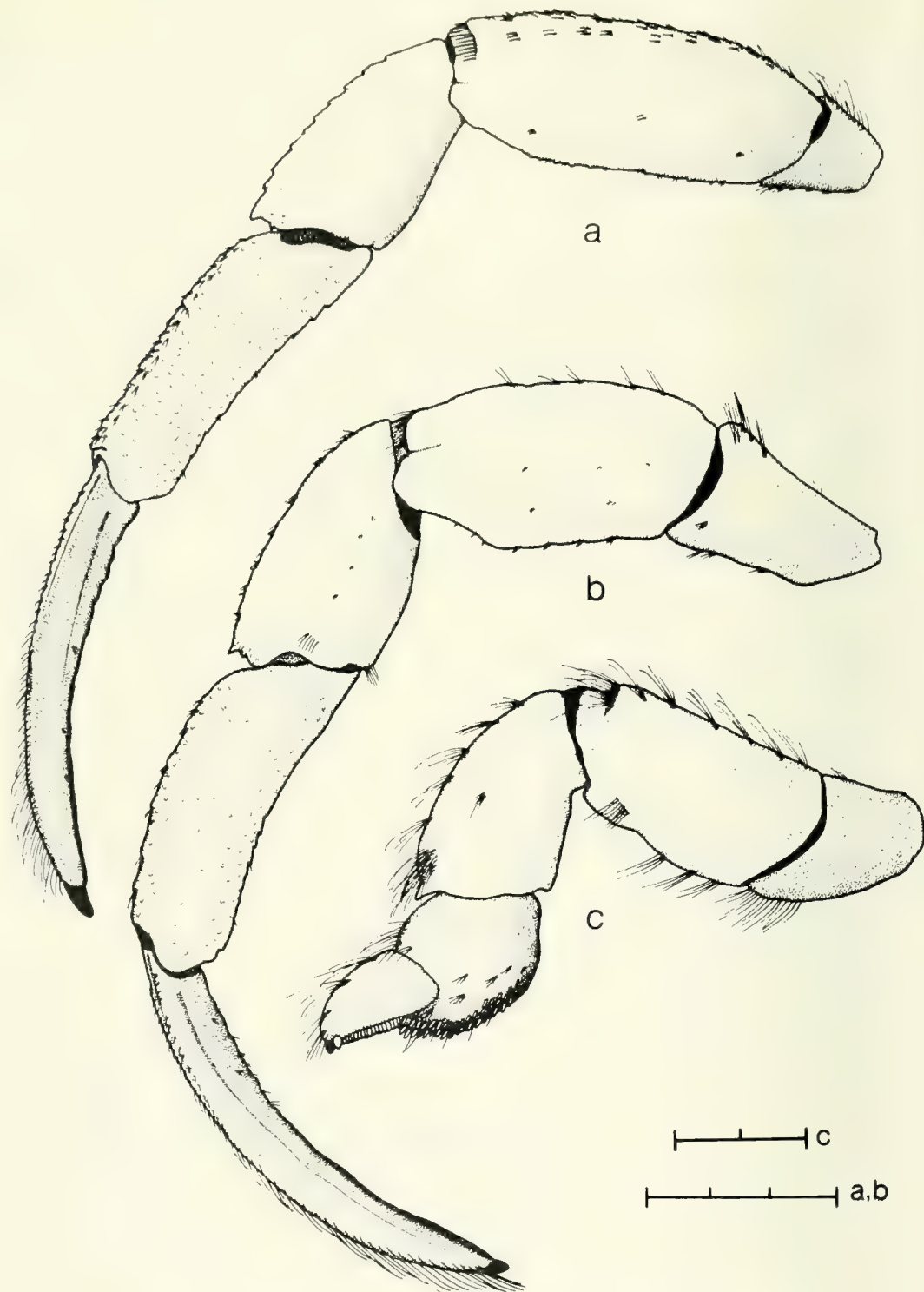


Figure 2. *Pagurus mertensii* Brandt s.s. ♂ (SL = 4.5 mm), from Pribilof Is.: a, left P₂ (lateral view); b, left P₃ (lateral view); c, left P₄ (lateral view). Scales equal 3 mm (a,b) and 1 mm (c) (from McLaughlin, 1972).

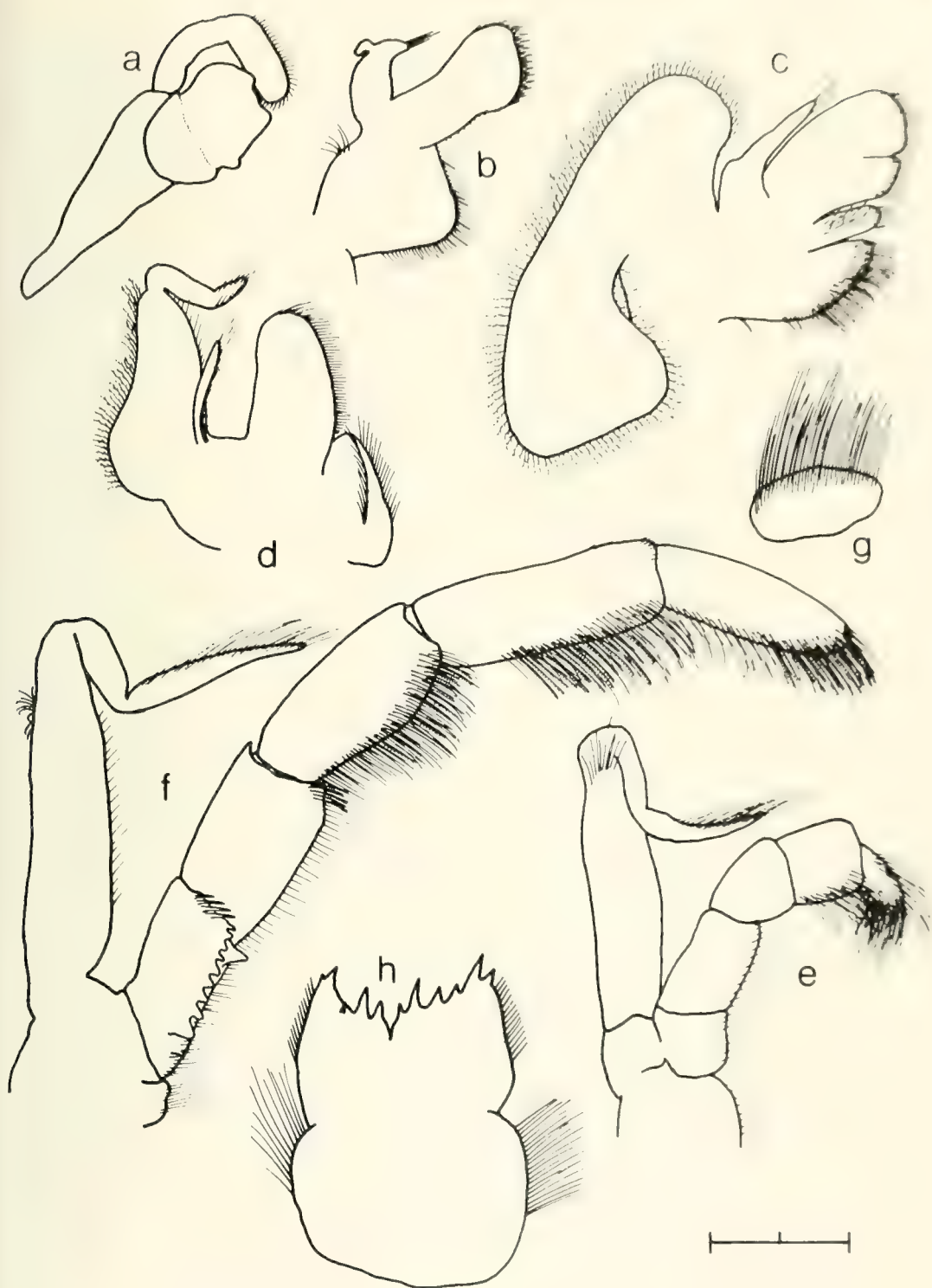


Figure 3. *Pagurus mertensii* Brandt s.s. ♂ (SL = 4.5 mm), from Pribilof Is., a-f, mouthparts (left, internal face): a, mandible; b, maxillule; c, maxilla; d, mxp; e, mxp; f, mxp—g, sternite P₃; h, telson. Scale equals 1 mm (from McLaughlin, 1972).

TABLE 1. Comparative Diagnostic Characters of *Parapagurodes*, *Pagurodes*, and *Acanthopagurus*

Character	<i>Parapagurodes</i>	<i>Pagurodes</i>	<i>Acanthopagurus</i>
Branchial lamellae	phyllobranchiate	trichobranchiate	phyllobranchiate
Ocular acicles	moderately broad, triangular or subtriangular; terminal spine submarginal	narrowly triangular; terminal spine marginal or submarginal	moderately narrow, triangular; terminal spine marginal
Antennular peduncle, dorsodistal surface ultimate segment	naked or with 1 or 2 setae	row of stiff setae	row of stiff setae
Maxillule, external endopodal lobe	moderately well-developed, not recurved	vestigial or absent	moderately well-developed, not recurved
Sternite P ₃ , anterior margin	unarmed	with few small spines	with few small spines
Coxae P ₃ ♂	symmetrical	symmetrical	asymmetrical
Sexual tubes	right, short	right, moderately long	right, short
Pleopods ♂	absent or weakly developed	weakly developed	well-developed
Telson Posterior lobes	terminal margins straight or slightly concave, with small spines and spinules	terminal margins strongly oblique, with several strong spines	terminal margins somewhat oblique, with few small spines or spinules

short sexual tube; no paired pleopods, pleopods pl₁ to pl₅ biramous with rami weakly developed, or absent. Females with paired gonopores; no paired pleopods, biramous pleopods, pl₂ to pl₄ weakly or moderately well-developed, pl₅ weakly developed or absent. Uropods asymmetrical. Telson with terminal margins generally straight, slightly concave, or slightly oblique, with row of small spines or spinules. Sternite of third pereopods with anterior margin unarmed.

AFFINITIES.—*Parapagurodes* appears most closely related to the genera *Pagurodes* Henderson, 1888, as restricted by de Saint Laurent (1969) to the type species, *Pagurodes inarmatus* Henderson, and *Acanthopagurus* de Saint Laurent, 1968. Comparative studies of *Acanthopagurus* (de Saint Laurent, personal communication) and of two syntypes of *Pagurodes inarmatus* (BM) have shown that although these three genera share many characters of gross morphology in common, several diagnostic characters justify their distinctness (see Table 1). In addition, the prezoeae of the two species of *Parapagurodes*, as determined from dissections of eggs nearing hatching, show that the larval development of this genus differs distinctly from that of *Acanthopagurus*, as described by de Saint Laurent (1969) for *Acanthopagurus dubius* (A. Milne-Edwards and

Bouvier). The condition of these prezoeae was too poor to permit full descriptions of the stage; however, three distinctions between the larvae of the two genera can be made. The larvae of *Parapagurodes* lack the prominent posterolateral spines present on the carapace of *A. dubius*; the rostrum, at least in *P. makarovi*, is considerably longer than that of *A. dubius*; and the telsons of the two species of *Parapagurodes* (Figs. 4a, b) are distinctly different from that of *A. dubius* (cf. de Saint Laurent, 1969, fig. 18).

VARIATIONS.—Among the characters recommended for generic evaluations within the Paguridae (cf. de Saint Laurent-Dehancé, 1966; de Saint Laurent, 1970b), particular significance has been placed on the presence or absence of sexual tubes. In those genera possessing sexual tubes, either paired or unpaired, additional significance has been attached to the relative length of the tube, its orientation, i.e., curved toward the interior or exterior, or directed anteriorly or posteriorly; and in those species having unpaired tubes, the occurrence of the tube on the right or the left coxa. In the two species of *Parapagurodes*, the males exhibited considerable variation, particularly in the orientation of the sexual tube. Although approximately one-half

of the specimens had sexual tubes on the right coxae which were oriented toward the exterior, the remainder had tubes oriented to the posterior, anterior, or interior. In a few instances the tubes were much shorter than would have been expected for mature animals, and in one instance (*P. makarovi*, Fig. 7c) a specimen was found to have paired sexual tubes, both oriented toward the exterior. There is little doubt that the possession of sexual tubes is of generic significance in the Paguridae; however, it must be pointed out that considerable variation does occur, both within species and within genera. Whether such observed variation is the result of normal variation within a population or is the result of artifacts of preservation has not yet been ascertained.

Variation in the number of unpaired pleopods in both males and females is also characteristic of *Parapagurodes*. Most frequently, males of *P. makarovi* lacked any vestige of pleopods; however, small males of this species often were observed with vestigial pleopods. Similarly, females of this species normally possessed weakly developed pleopods, pl_2 to pl_4 , with pl_5 absent. Small specimens, however, occasionally had vestigial fifth pleopods. In contrast, males of *Parapagurodes laurentae* n. sp. normally were observed with biramous pleopods, pl_3 to pl_5 , weakly developed; only rarely were the pleopods absent. The females of this species usually had well developed, biramous pleopods, pl_2 to pl_4 , with pl_5 reduced, as in the males; however, occasionally, specimens were observed with poorly developed pleopods, pl_2 to pl_4 , and with pl_5 vestigial or absent. Both species had a relatively high percentage of specimens infected with an abdominal bopyrid parasite, *Stegophryxus* n. sp. (Markham, in press); however, no correlation between parasitic infestation and pleopod variation could be determined.

A third variable character of this genus is seen in the fourth pereopods. Typically, in *P. makarovi* the fourth pereopods are not subchelate, whereas in *P. laurentae* they are weakly subchelate; however, occasionally specimens of *P. makarovi* were observed with subchelate fourth pereopods, and conversely, specimens of *P. laurentae*, infrequently had fourth pereopods which were not subchelate.

DISCUSSION.—As previously indicated, Holmes (1900) placed the species, identified by Benedict as *Eupagurus mertensii* (Brandt), in the genus *Parapagurus*. His generic designation was

based upon his examination of a single female specimen which he believed possessed trichobranchiate branchial lamellae. All recent efforts to locate the specimen upon which Holmes based this conclusion have been unsuccessful. The remainder of Benedict's identified specimens have been reexamined, and none have been found with trichobranchiate branchial lamellae. Neither do the females have the single gonopore, nor the males the paired first and second pleopods usually characteristic of species of *Parapagurus*. It has been necessary, therefore, to establish a new genus, *Parapagurodes*, for Holmes' species and one additional new species from California. The genus is so named because of its close affinity with Henderson's (1888) genus *Pagurodes*.

Parapagurodes makarovi, new species

Figures 4a, 5–8

Eupagurus (*Labidochirus*) *mertensii*: Benedict, 1892, p. 2 [by implication] [not *Pagurus Mertensii* Brandt, 1851].

Parapagurus Mertensii Holmes, 1900, p. 155.

Parapagurus mertensii: Rathbun, 1904, p. 162, pl. 5, fig. 6; 1910, p. 162, pl. 5, fig. 6.—Alcock, 1905 [in part], p. 172.—Schmitt, 1921, p. 146, pl. 16, fig. 5.—Makarov, 1938, p. 226, fig. 75; 1962, p. 214, fig. 75.—Gordan, 1956 [in part], p. 338 (see discussion).

not *Parapagurus mertensii*: Taylor, 1912, p. 205.—Hart, 1940, p. 103. [? = *Pagurus hirsutiusculus hirsutiusculus* (Dana, 1851)].

HOLOTYPE.—♂ (SL = 4.0 mm), USNM 16709.

PARATYPES.—See table 2.

TYPE LOCALITY.—Off Anacapa I., California. "Albatross" station 2946, 33° 58' 00" N, 119° 30' 45" W, 274 m.

DESCRIPTION.—Shield length equalling or slightly exceeding width, or rarely, width slightly exceeding length; anterolateral margins sloping; anterior margin between rostrum and lateral projections straight, sloping, or slightly concave; posterior margin rounded or roundly truncate; dorsal surface usually convex, slightly rugose anteriorly, and usually with few scattered tufts of short setae, occasionally moderately setose; anterolateral angle produced, blunt or with small spine or spinule. Rostrum usually elongate or moderately elongate, considerably exceeding lateral projections, triangular, slender or moderately broad; terminating subacutely or with small spinule; frequently slightly elevated in midline to form very weak keel, tip often depressed. Lateral projections broadly rounded or obtusely triangular, or infrequently obsolete, with very small submarginal spine or spinule or less frequently, unarmed.

Ocular peduncles short, equalling or slightly ex-

TABLE 2. *Parapagurodes makarovi*, n. sp., Material Examined

Locality	Depth (m)	Station	Date	Sex			SL (mm)
		Deposition		♂	♀	♀ ♀	
<i>California</i>							
36°52'00"N, 122°11'00"W	119	Albatross 3125 (USNM 52506)	13/3/90	1			3.3
36°26'40"N, 122°00'05"W	141	Albatross 3184 (USNM 16711)	3/4/90	1			5.0
Point Pinos Light	119–554	Albatross 4471 (USNM)	14/5/04	1			4.0
Point Pinos Light	137–198	Albatross 4523 (USNM)	26/5/04	1			4.5
34°06'45"N, 120°18'00"W	101	Albatross 2959 (USNM 42612)	9/2/89	1			3.3
34°02'30"N, 119°21'10"W	86–141	Velero III 1420–41 (AHF)	17/9/41	1			2.4
34°01'55"N, 119°26'40"W	82–86	Velero III 1419–41 (AHF)	17/9/41	1			3.5
34°01'30"N, 119°21'00"W	82	Velero III 874–38 (AHF)	1/8/38	1			3.1
E. Pt., San Nicholas I.	620	Albatross 4423 (USNM)	13/4/04			1	4.6
E. Pt., San Nicholas I.	532	Albatross 4421 (USNM)	12/4/04			1	3.1
33°58'00"N, 119°30'45"W	274	Albatross 2946 (USNM 16709; 42631)	7/2/89	2	2		3.0–4.0
33°56'00"N, 119°40'30"W	238–421	Velero III 992–39 (AHF)	10/8/39	2	2	1	1.8–4.0
33°55'40"N, 119°47'07"W	117–252	Velero III 1195–40 (AHF)	31/10/40	1	1	1	2.3–2.7
33°55'30"N, 119°41'30"W	486	Albatross 2948 (USNM 16710)	7/2/89	10	8	1	3.1–4.6
33°46'20"N, 119°58'15"W	196–229	Velero III 1393–41 (AHF)	26/8/41		1		3.1
33°43'30"N, 119°09'20"W	128	Velero III 983–39 (AHF)	29/5/39	1			3.5
33°40'55"N, 119°50'10"W	130–139	Velero III 1385–41 (RMNH)	25/8/41	3		1	3.0–4.0
Brockway Pt. Santa Rosa I.	75	Albatross 4431 (USNM 52507)	15/4/04			1	2.5
33°37'45"N, 119°08'02"W	146–148	Velero III 982–39 (AHF)	29/5/39			1	2.1
33°34'40"N, 119°00'15"W	139–159	Velero III 981–39 (AHF)	29/5/39	5	1		2.5–3.3
33°33'27"N, 119°04'00"W	256–296	Velero IV 2062–51 (AHF; MNHN)	18/10/51		3	2	2.5–3.3
33°29'30"N, 119°06'45"W	183	Velero III 1176–40 (AHF)	9/9/40	1			3.2
33°26'00"N, 118°21'35"W	262–406	Velero III 1434–41 (AHF)	26/10/41	1			3.1
33°24'30"N, 118°21'10"W	165–185	Velero III 1000–39 (AHF)	12/8/39	1			1.6
33°24'15"N, 117°59'35"W	208–240	Velero III 1213–40 (AHF)	30/11/40	1			3.1
33°23'45"N, 118°20'15"W	73–146	Velero III 908–39 (AHF)	28/1/39			1	2.5
33°23'30"N, 118°19'20"W	221–475	Velero III 1029–39 (RMNH)	10/12/39	1	1		2.1–3.5

TABLE 2. (Continued)

Locality	Depth (m)	Station Deposition	Date	Sex			SL (mm)
				♂	♀	♀ ♀	
33°20'20"N, 118°16'10"W	179-212	Velero III 1150-40 (AHF)	4/7/40	2	2	1	2.4-3.1
33°18'25"N, 118°15'30"W	152-229	Velero III 1028-39 (AHF)	10/12/39	1		1	2.3-2.4
33°16'55"N, 118°13'55"W	197-210	Velero III 1173-40 (AHF)	20/8/40	1	1		3.4-3.6
33°16'00"N, 118°13'55"W	187-205	Velero IV 2136-52 (AHF)	24/7/52	3	1		2.9-3.5
33°16'00"N, 118°16'40"W	183-192	Velero III 1322-41 (AHF)	18/5/41	1			2.8
33°15'55"N, 118°13'50"W	214-234	Velero III 1151-40 (MNHN)	5/7/40	6			1.9-3.1
33°15'30"N, 118°12'25"W	265-274	Velero III 1172-40 (BM)	20/8/40	2			3.0-3.1
33°15'00"N, 118°11'35"W	265-283	Velero III 1188-40 (AHF)	29/9/40	1	1		2.1-2.9
33°03'10"N, 118°40'30"W	247-274	Velero III 1020-39 (AHF)	24/11/39	1	1	2	2.1-3.1
33°01'10"N, 118°32'10"W	110-247	Velero III 1016-39 (AHF)	23/11/39	1			2.1
33°00'45"N, 118°42'00"W	91-274	Velero III 1018-39 (BM)	23/11/39	4		1	1.8-2.4
33°00'30"N, 120°29'00"W	329	Albatross 2898 (USNM 16708)	6/1/89	1			2.6
33°00'20"N, 118°33'10"W	110-155	Velero III 911-39 (AHF)	18/2/39	2	1	2	2.3-2.8
32°59'30"N, 118°38'25"W	216-384	Velero III 1026-39 (AHF)	9/12/39	4	1	1	2.4-3.2
Point Loma Light	[91]	Albatross 4311 (USNM)	4/3/04			1	3.3
<i>West Coast Baja California, Mexico</i>							
28°12'05"N, 115°33'20"W	130-174	Velero III 1010-39 (AHF)	20/9/39	1		1	2.4-2.9
28°12'00"N, 115°33'33"W	159-174	Velero III 1119-40 (AHF)	19/2/40		1		3.1
28°00'00"N, 115°28'43"W	115-119	Velero III 1254-41 (AHF)	26/2/41	1			2.5

ceeding one-half shield length, stout; strongly inflated basally with corneae dilated; surface with scattered tufts of short setae. Ocular acicles prominent, triangular or subtriangular, narrow or moderately broad, with dorsal surface slightly concave; terminating acutely or subacutely, with strong submarginal spine; separated basally by one to two times basal width of one acicle.

Antennular peduncles long, exceeding ocular peduncles by one-third to one and one-third length of ultimate segment; ultimate segment with one or two short setae on dorsal surface distally; penultimate segment with few scattered, short setae; basal segment with strong, acute spine at ventrodistal margin, dorsolateral margin with small spine.

Antennal peduncles moderately long, exceeding

ocular peduncles by one-third to two-thirds length of ultimate segment; with supernumerary segmentation (cf. McLaughlin and Provenzano, in press). Fifth segment usually unarmed, occasionally with minute spinule on midventral margin, and with scattered tufts of short, stiff setae. Fourth segment unarmed, with few tufts of stiff setae. Third segment with very strong spine at ventrodistal margin and tufts of stiff setae. Second segment with dorsolateral distal angle produced, terminating in strong, simple or occasionally small bifid spine, lateral and mesial margins usually unarmed, occasionally mesial margin with small spine or spinule; dorsomesial distal angle with strong spine, mesial face with few stiff setae and often with two or three small spinules. First segment with spine on lateral surface distally;

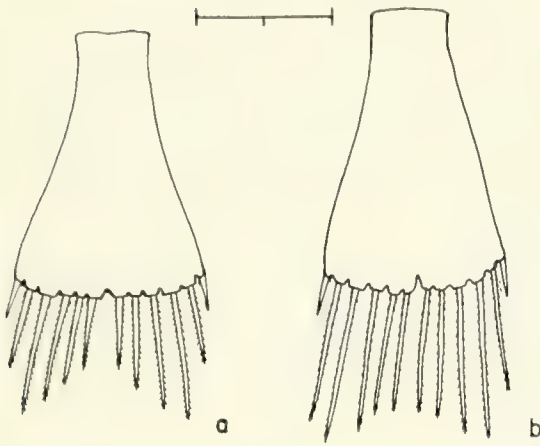


Figure 4. Telson of prezoal stage: a, *Parapagurodes makarovi*, n. sp.; b, *Parapagurodes laurentae*, n. sp. Scale equals 0.2 mm.

ventral margin produced, usually with one to four moderately strong spines laterally, occasionally unarmed. Antennal acicle long, considerably exceeding length of ocular peduncles and frequently equalling length of antennal peduncles; terminating in strong, acute spine; mesial margin and dorsal surface with tufts of stiff setae. Antennal flagella long, equalling or overreaching tip of right cheliped; naked or with intermittent, short bristles.

Mandible without distinctive characters. Maxillule with proximal endite tapered distally; endopodite with one or two bristles on weakly produced internal lobe, external lobe usually moderately well-developed, not recurved. Maxilla with endopodite approximately equalling scaphognathite in distal extension, distally tapered. First maxilliped with flagellum of exopodite very short, slender. Second maxilliped with basis-ischium fusion apparently incomplete. Third maxilliped with basis-ischium fusion incomplete; basis usually with one to four moderately strong spines, occasionally unarmed; merus with strong spine at dorsodistal margin, ventral margin with one strong spine, or rarely unarmed; carpus with strong spine at dorsodistal margin. Sternite of mxp₃ with one or less frequently two spines on either side of midline, and with row of long setae.

Right cheliped elongate, moderately slender, particularly in large specimens; surfaces usually with scattered tufts of short to moderately long setae. Dactyl moderately long, one-half to three-fourths length of palm, set at slightly oblique angle to palm; terminating in small corneous claw; cutting edge with row of strong, calcareous teeth, often replaced distally by short row of small, corneous teeth; slightly overlapped by fixed finger; dorsomesial margin with row of small spinules or spinulose tubercles, decreasing in size distally, dorsal

surface elevated proximally into weak ridge or keel with irregular row of small spinules or tubercles becoming obsolete distally, often also with few scattered, small spinules or tubercles mesiad of keel proximally; mesial and ventral surfaces usually unarmed. Palm elongate, slightly shorter than or equalling length of carpus, moderately slender, particularly in large specimens, moderately inflated dorsoventrally; dorsal surface usually strongly convex, proximally unarmed or with low protuberances or spinules, more prominent laterally and mesially, and with small, simple or multidenticulate spinules or spinulose tubercles distally and on fixed finger; dorsomesial margin with row of small spines or spinulose tubercles; dorsolateral margin with row of small spines or spinulose tubercles increasing in size on fixed finger, occasionally obsolete proximally, lateral face with few scattered, low protuberances; ventral surface somewhat concave mesiad of midline and with irregular rows of low protuberances; mesial face usually unarmed. Carpus long, equalling or frequently exceeding length of merus, moderately slender; dorsomesial margin with row of usually strong, acute spines, dorsal surface generally convex, with row of small to strong spines mesiad of midline and extending from proximal margin distally one-third to two-thirds length of carpus and with second, longitudinal row of usually small spines laterad of midline extending from distal margin proximally one-half to two-thirds, or occasionally entire length of surface, distal margin usually with few small spines or spinules; dorsolateral margin not delimited or with single or double, irregular row of small spinules or tubercles, often obsolete proximally; lateral face often with scattered, small, usually multidenticulate tubercles or protuberances, distal margin occasionally with few small denticles; mesial face unarmed or with few small spinules dorsally; ventral surface usually with scattered, small spines or spinulose protuberances, occasionally unarmed, ventromesial margin frequently with row of small, often multidenticulate spinules or tubercles. Merus subtriangular; dorsal surface with irregular rows of transverse, occasionally multidenticulate protuberances, distal margin with one to several small spines and spinules; mesial face usually with few transverse, occasionally spinulose ridges dorsally and transverse rows of moderately prominent spines ventrally, ventromesial margin with row of moderately strong or strong spines; ventral surface unarmed or with one or two strong spines; lateral face with transverse, multidenticulate ridges or protuberances, distal margin usually with one moderately prominent spine and numerous denticles or spinules dorsally and small spines or spinulose tubercles ventrally, ventrolateral margin with row of strong, acute spines, increasing in size distally. Ischium with or frequently without row of small spines on ventromesial margin, ventrolateral margin usually with one or

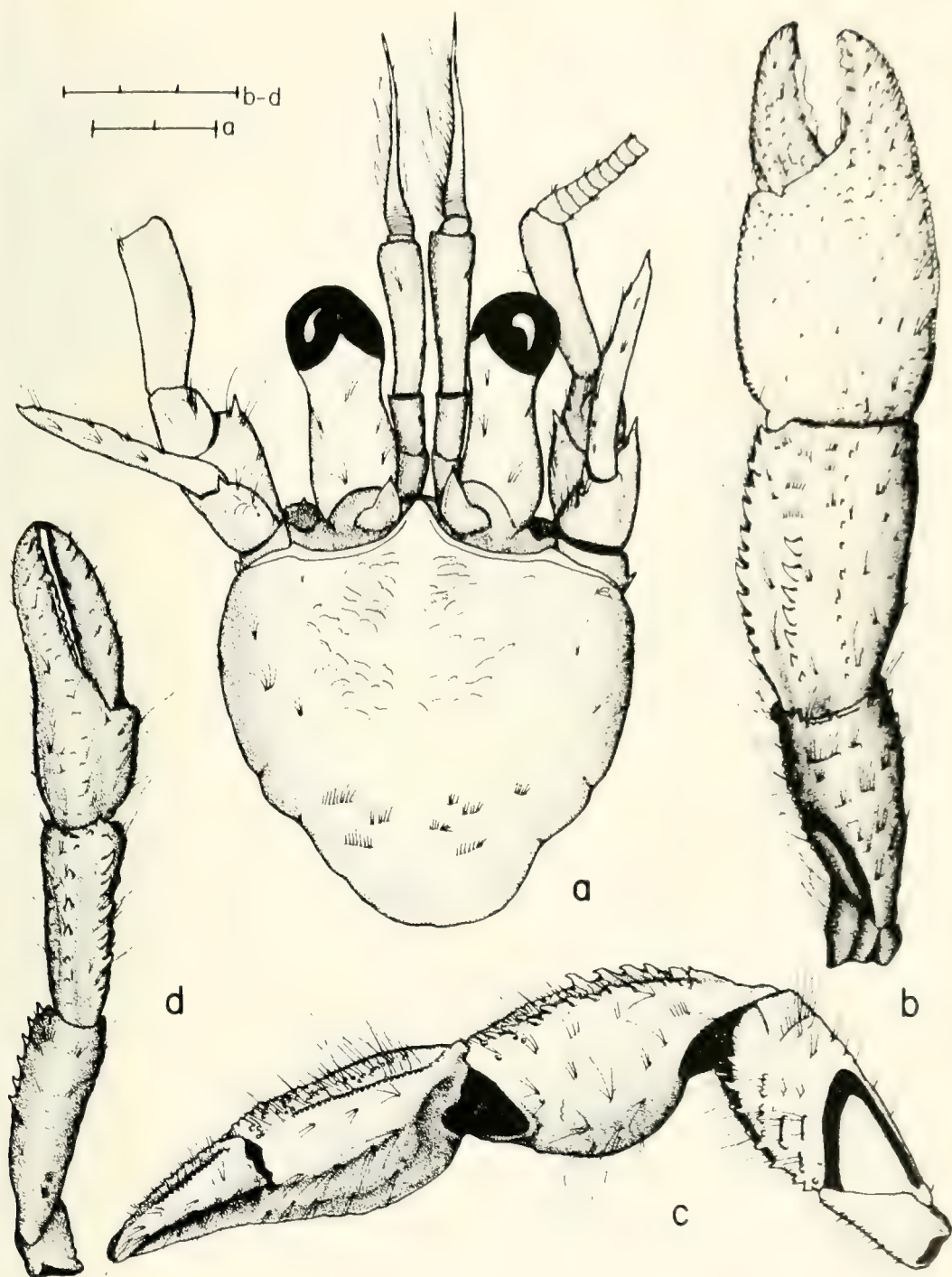


Figure 5. *Parapagurodes makarovi*, n. sp. ♂ (SL = 3.5 mm), "Velero IV" sta. 2136-52: a, shield; b, right cheliped (dorsal view); c, right cheliped (mesial view); d, left cheliped (dorsal view). Scales equal 1 mm (a) and 3 mm (b-d).

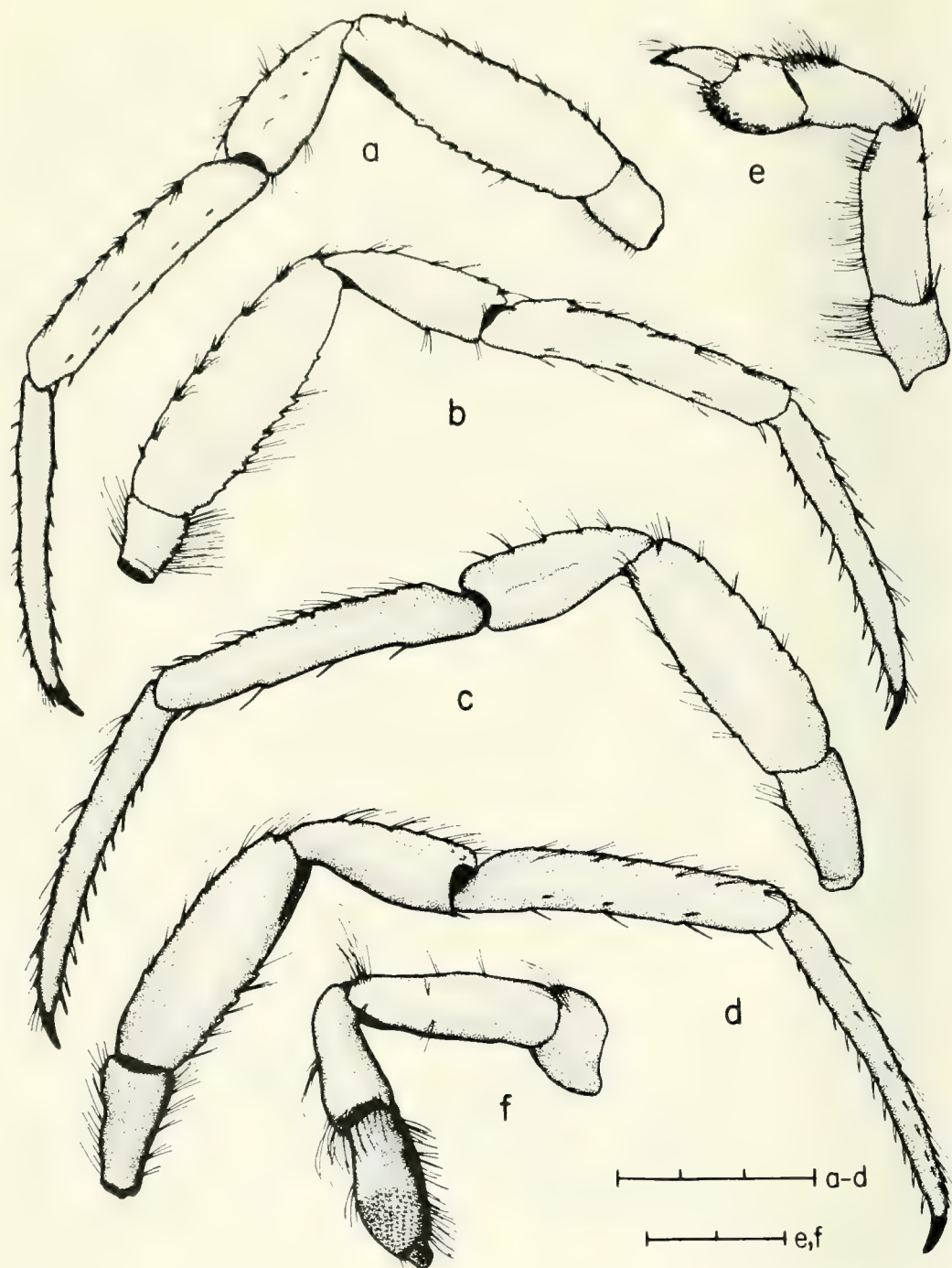


Figure 6. *Parapagurodes makarovi*, n. sp. ♂ (SL = 3.5 mm) "Velero IV" sta. 2136-52, a, b, P₂: a, lateral view; b, mesial view.—c, d, P₂: c, lateral view; d, mesial view.—e, P₃, lateral view; f, P₃, lateral view. Scales equal 3 mm (a-d) and 1 mm (e, f).

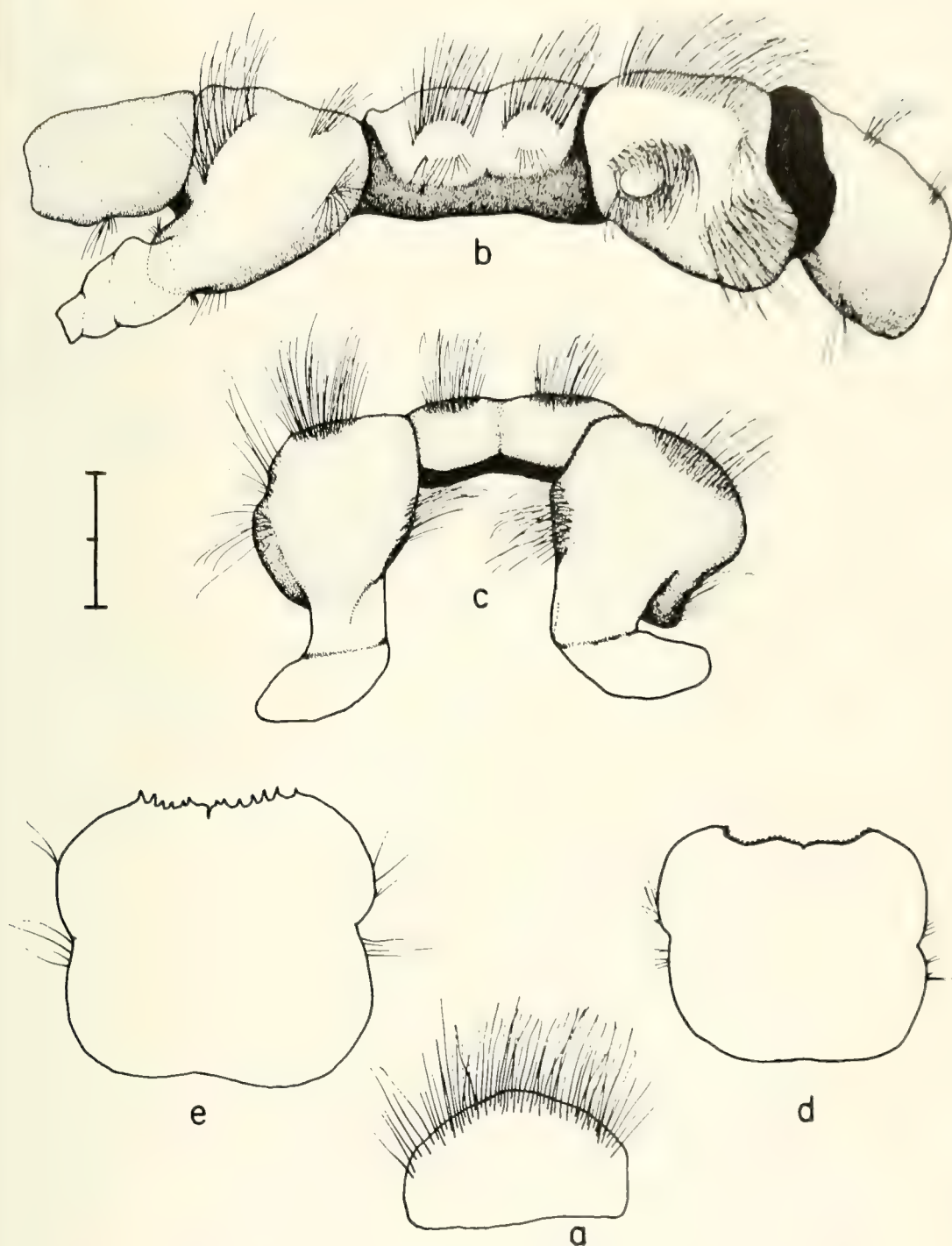


Figure 7. *Parapagurodes makarovi*, n. sp.: a,b,d, ♂ (SL = 3.5 mm), "Velero IV" sta. 2136-52; a, sternite P₃; b, coxae and sternite P₃; d, telson.—c: ♂ (SL = 3.6 mm), "Albatross" sta. 2948, USNM 16710, coxae and sternite P₃.—e: holotype, ♂ (SL = 4.0 mm), "Albatross" sta. 2946, USNM 16709, telson. Scale equals 0.5 mm.

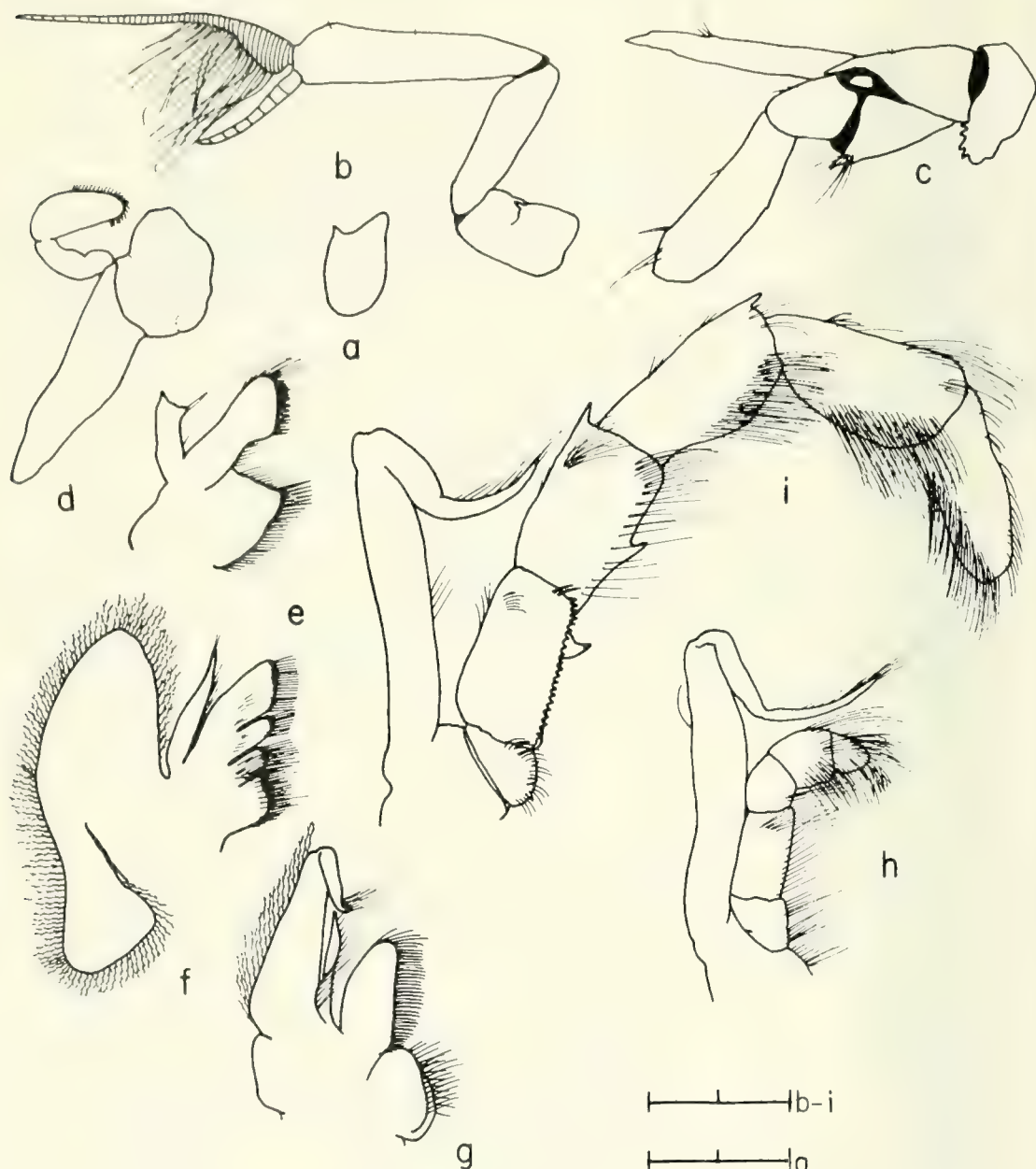


Figure 8. *Parapagurodes makarovi*, n. sp.: a-c ♂ (SL = 3.5 mm), "Velero IV" sta. 2136-52; a, branchial lamella; b, antennular peduncle; c, antennal peduncle.—d-i, ♀ (SL = 4.5 mm), "Albatross" sta. 2894, mouthparts (internal face): d, mandible; e, maxillule; f, maxilla; g, mxp₁; h, mxp₂; i, mxp₃. Scales equal 0.5 mm (a) and 1 mm (b-i).

two short, transverse rows of small spinules, extending onto lateral face ventrally. Coxa unarmed.

Left cheliped elongate, usually reaching to distal half of right, slender; dactyl and fixed finger, in dorsal view, frequently skewed laterally and strongly arched ventrally; surfaces with scattered tufts of moderately long setae. Dactyl long, two to two and

one-half times length of palm; terminating in strong, corneous claw; cutting edge with row of small, corneous teeth; slightly overlapped by fixed finger; dorsomesial margin unarmed or occasionally with few minute spinules proximally, dorsal, mesial, and ventral surfaces unarmed. Palm moderately long, one-half to two-thirds length of carpus; dorsal sur-

face convex, elevated in midline proximally, unarmed or with very small spinules or spinulose protuberances; dorsolateral margin with row of small spines or tubercles, increasing in size on fixed finger but becoming obsolete distally, dorsomesial margin with single or double row of minute spinules or unarmed; lateral, mesial, and ventral surfaces unarmed. Carpus moderately long, two-thirds to three-fourths length of merus, subrectangular; dorsolateral and dorsomesial margins each with row of moderately strong spines, usually strongest mesially, distal margin with one or two moderately strong spines; lateral face with longitudinal row of small spinules or denticles dorsally, ventrolateral margin usually with one to several small spinules; mesial face with irregular, transverse rows of spinulose protuberances or tubercles, ventromesial margin with irregular row of small spinules; ventral surface occasionally with one or two small spinules. Merus subtriangular; dorsal surface with irregular row of transverse ridges, distal margin unarmed or with one moderately small spine; lateral face usually slightly spinulose or denticulate, ventrolateral margin with single or double row of moderately strong or strong spines; mesial face often with transverse rows of spinules or spinulose protuberances ventrally, ventromesial margin with row of moderately strong spines, decreasing in size distally. Ischium usually with row of small spinules or denticles on ventromesial margin, ventral surface often with few small spinules. Coxa unarmed.

Second and third pereopods elongate, usually reaching to base of dactyl of right cheliped, occasionally reaching to tip, slender, somewhat laterally compressed; dorsal surfaces and ventral margins of meri and ischia usually with tufts of long, stiff setae. Dactyls moderately long, two-thirds to one and one-third length of propodi; in lateral view, straight or slightly curved ventrally; in dorsal view, straight; terminating in strong, corneous claw; dorsal surfaces frequently each with few, small, corneous spines; lateral faces each usually with row of small, corneous spinules dorsally; mesial faces unarmed; ventral margins each with row of strong, corneous spines, increasing in size distally. Propodi elongate, one and one-third to one and one-half times length of carpi; dorsal surfaces each with row of low, occasionally spinulose protuberances; lateral and mesial faces unarmed or often with row of small, corneous spinules ventrally; ventral margins each frequently with row of long, corneous spines or spinulose bristles and one or two corneous spines distally. Carpi moderately short, one-half to two-thirds length of meri; dorsal surfaces each with small spine or spinule distally, and frequently with row of low protuberances; lateral, mesial, and ventral surfaces usually unarmed, occasionally ventral surfaces with minute spinules. Meri laterally compressed; dorsal margins each with row of low, occasionally spinulose protuberances; mesial and

lateral faces usually unarmed; ventral margin with single or double row of moderately strong spine (P_2) or row of small spines, or unarmed (P_3). Ischia unarmed or with row of small spines or denticle. Coxae unarmed.

Fourth pereopods usually not subchelate, occasionally weakly subchelate. Dactyls with very small preungual process on lateral face; propodal rasp with one to three irregular rows of corneous scale.

Fifth pereopods chelate; coxae symmetrical.

Sternite of third pereopods subsemicircular or semicircular, anterior margin with row of long, stiff setae.

Males with well developed, short sexual tube on right, occasionally with vas deferens of left slightly produced, rarely with well developed short sexual tube also on left. No paired pleopods, unpaired pleopods usually absent in adults, occasionally with weakly developed, biramous pleopods pl_2 and pl_1 .

Females with paired gonopores; no paired pleopods, unpaired pleopods, pl_2 to pl_1 , usually weakly developed, pl_2 absent or infrequently rudimentary.

Uropods asymmetrical. Telson with posterior lobes generally symmetrical; separated by very small, shallow, median cleft; terminal margins straight or somewhat concave, each with several to numerous small or very small spines or spinules, lateral margins with tufts of moderately long setae; anterior lobes unarmed, margins with tufts of setae.

COLORATION.—Living color unknown. In preservative: Body and appendages straw-colored.

DISTRIBUTION.—Southern California, Monterey Bay, to west coast of Baja California peninsula, Mexico: 75 to 574 meters.

AFFINITIES.—*Parapagurodes makarovi*, although having a superficial similarity with *Pagurus mertensii* s.s., is most closely related to *Parapagurodes laurentae*, n. sp. It may be distinguished from this latter species by the absence of strong spines on the dorsal surfaces of the palms of the left and right chelipeds.

ETYMOLOGY.—This species is named for the Russian carcinologist, V. V. Makarov, who first distinguished this species from *Pagurus mertensii* Brandt.

DISCUSSION.—As previously indicated, Holmes (1900) incorrectly assigned the California species misidentified by Benedict as *Eupagurus mertensii* (Brandt) to the genus *Parapagurus*. It is obvious that both Benedict and Holmes considered this species synonymous with that described by Brandt. Makarov (1938, 1962) interpreted Brandt's species to be synonymous with *P. h. hirsutiusculus* (Dana) and chose to submerge the name *mertensii* out of preference for Dana's more commonly used, junior synonym. As this species differed significantly from Holmes' *Parapagurus mertensii*, Makarov retained the latter species without

TABLE 3. *Parapagurodes laurentae* n. sp., Material Examined

Locality	Depth (m)	Station	Date	Sex			SL (mm)
		Deposition		♂	♀	♀ ♀	
California							
34°03'50"N, 119°45'25"W	66–86	Velero III 1303–41 (AHF)	12/4/41	1		1	1.4–1.9
34°01'32"N, 119°27'10"W	69–79	Velero IV 1937–50 (AHF)	24/3/50	3		4	1.5–2.3
33°53'10"N, 119°55'00"W	93–97	Velero III 1290–41 (AHF)	11/4/41	1			2.9
33°34'40"N, 119°00'15"W	139–159	Velero III 981–39 (AHF)	29/5/39	5	10		2.0–3.2
33°29'10"N, 119°00'00"W	66–88	Velero III 1146–40 (AHF)	1/7/40	3			1.9–3.4
33°29'N, 119°01'W	73	Velero III 895–38 (AHF)	12/8/38	2			3.4–3.5
33°27'35"N, 119°02'35"W	38–51	Velero III 978–39 (AHF)	28/5/39	2	3	1	1.9–3.4
33°27'20"N, 118°35'35"W	73–91	Velero III 1311–41 (AHF)	4/5/41	1			2.4
33°25'30"N, 118°22'55"W	141–210	Velero III 1371–41 (AHF)	20/7/41	2			1.8–1.9
33°25'15"N, 118°21'30"W	199–262	Velero IV 1618–48 (AHF)	16/10/48	3	2	4	1.6–3.0
33°24'30"N, 118°21'10"W	165–185	Velero III 1000–39 (AHF)	12/8/39	3	1	2	1.5–2.4
33°24'15"N, 117°59'35"W	208–240	Velero III 1213–40 (AHF)	30/11/40			1	2.7
Off Santa Catalina I.	152	_____ (AHF)	15/8/51		1		1.3
33°23'40"N, 118°19'50"W	183–198	Velero III 1359–41 (AHF)	13/6/41	1			1.5
33°23'30"N, 118°19'20"W	221–475	Velero III 1029–39 (AHF)	10/12/39	4	1		2.1–3.5
Santa Catalina I.	16–20	Velero IV 1648–48 (AHF)	1/12/48	1			1.9
33°20'20"N, 118°16'10"W	179–212	Velero III 1150–40 (AHF)	4/7/40	3	4	2	1.7–3.3
33°20'35"N, 118°17'15"W	150–161	Velero III 1149–40 (AHF)	4/7/40	2		1	1.4–1.6
33°18'25"N, 118°14'45"W	194–201	Velero III 1355–41 (AHF)	12/6/41	1	1		2.1–3.1
33°18'25"N, 118°15'30"W	152–229	Velero III 1028–39 (AHF)	10/12/39	8	6		1.9–3.5
33°18'10"N, 119°22'15"W	177–190	Velero III 1125–40 (AHF)	12/4/40		1		3.1
33°17'20"N, 118°14'00"W	187–212	Velero III 1353–41 (BM)	12/6/41	3		2	1.8–3.0
33°16'55"N, 118°13'55"W	197–210	Velero III 1173–40 (AHF)	20/8/40			1	2.4
33°16'30"N, 118°17'00"W	110–146	Velero III 1354–41 (AHF)	12/6/41	1	1		1.6–1.9
33°16'20"N, 118°15'20"W	159–174	Velero III 1429–41 (AHF 4127; RMNH; BM; MNHN; USNM 143007)	25/10/41	52	42		1.4–3.7
33°16'00"N, 118°13'55"W	187–205	Velero IV 2136–52 (RMNH; MNHN; AHF)	24/7/52	9	5		2.6–3.4

TABLE 3. (Continued)

Locality	Depth (m)	Station Deposition	Date	Sex			SL (mm)
				♂	♀	♀ ♀	
33°15'55"N, 118°13'50"W	214-234	Velero III 1151-40 (USNM 143010)	5/7/40	5		2	2.4-2.4
33°15'30"N, 118°15'05"W	190-247	Velero IV 1848-49 (AHF)	12/6/49		1	1	1.9-2.4
33°15'00"N, 118°11'35"W	265-283	Velero III 1188-40 (AHF)	29/9/40		1	1	2.1-2.3
33°14'15"N, 118°10'00"W	278-366	Velero III 1430-41 (AHF)	25/10/41	3	1	1	2.2-3.4
33°00'45"N, 118°42'00"W	91-274	Velero III 1018-39 (AHF)	23/11/39	6	3		1.9-3.3
33°00'30"N, 118°32'20"W	95-112	Velero III 1239-41 (AHF)	22/2/41		1		2.9
33°00'20"N, 118°33'10"W	110-155	Velero III 911-39 (AHF)	18/2/39	9	1	1	1.7-3.6
32°59'30"N, 118°38'25"W	216-384	Velero III 1026-39 (AHF)	9/12/39	1			3.1
32°46'30"N, 118°21'15"W	143-391	Velero III 914-39 (AHF)	19/2/39	4	2		2.4-3.1
32°45'55"N, 118°26'10"W	100-126	Velero III 1012-39 (AHF; USNM 143008)	9/11/39	7	3	2	1.6-2.6
32°35'00"N, 119°11'45"W	165-201	Velero III 1343-41 (AHF)	10/6/41	4	1		1.9-3.5
32°33'15"N, 117°22'05"W	143-148	Velero III 1240-41 (AHF)	23/2/41			3	1.9-2.5
<i>West coast Baja California, Mexico</i>							
28°12'35"N, 115°33'15"W	121-148	Velero III 1251-41 (AHF)	26/2/41	1			1.7
28°12'05"N, 115°33'20"W	130-174	Velero III 1010-39 (AHF)	20/9/39		1		1.4
28°05'45"N, 115°31'00"W	117-119	Velero III 1253-41 (AHF)	26/2/41	1			2.5
26°16'17"N, 113°41'03"W	99	Velero IV 1710-49 (AHF; USNM 143009)	7/3/49	12	1	3	1.8-2.7
<i>Gulf of California</i>							
28°00'02"N, 111°24'40"W	201	Velero III 735-38 (AHF)	29/3/37	1		2	2.4-2.9

change. In accordance with the Rules of Zoological Nomenclature (article 49), the name *mertensii* cannot be retained for Holmes' species even though it is now being transferred to yet another genus.

The references of both Alcock (1905) and Gordan (1956) refer, in part, to *Parapagurodes makarovi* and, in part, to *Pagurus mertensii* [sensu lato]. The distributions recorded by Rathbun (1904, 1910) and Schmitt (1921) of Kamchatka, Alaska and British Columbia are erroneous, and reflect the misidentification of this species by Benedict and Holmes. Taylor's (1912) record of *Parapagurus mertensii* from southern

British Columbia, which was repeated by Hart (1940), was most probably based on misidentifications of specimens of *Pagurus h. hirsutiusculus*.

Parapagurodes laurentae, new species

Figures 4b, 9-11

?*Pagurus* [sp]: Menzies and Miller, 1954, p. 153 (see discussion).

HOLOTYPE.—♂ (SL = 3.5 mm), AHF 4127.

PARATYPES.—See table 3.

TYPE LOCALITY.—2½ mi SE of Seal Rocks, Santa Catalina I., California, 33° 16' 20" N, 118° 15' 20" W, Velero III station 1429-41, 159-174 m.

DESCRIPTION.—Shield slightly longer than broad, or less frequently, length equalling width.

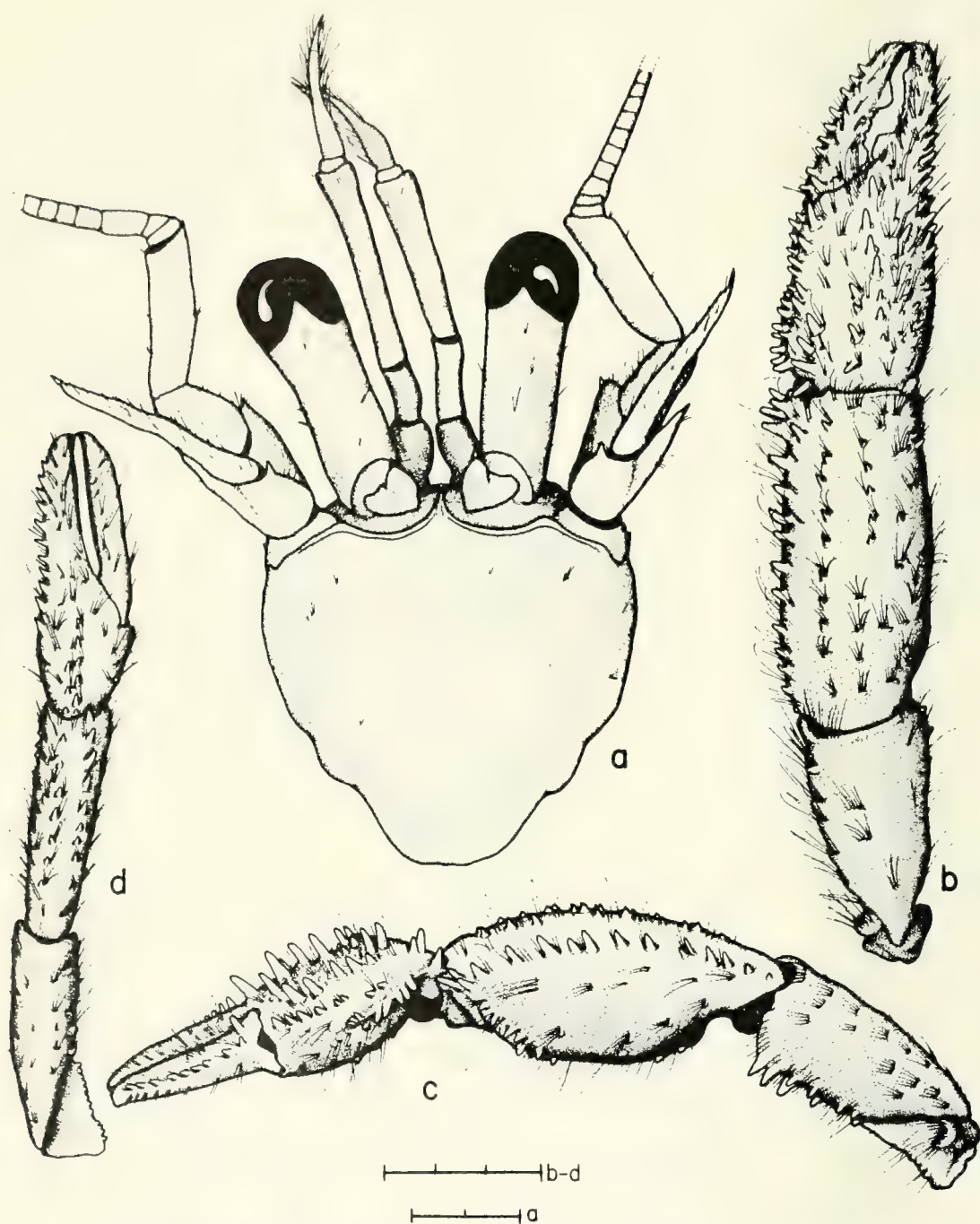


Figure 9. *Parapagurodes laurentae*, n. sp., paratype, ♂ (SL = 3.2 mm), "Velero III" sta. 1429-41: a, shield; b, right cheliped (dorsal view); c, right cheliped (mesial view); d, left cheliped (dorsal view). Scales equal 1 mm (a) and 3 mm (b-d).

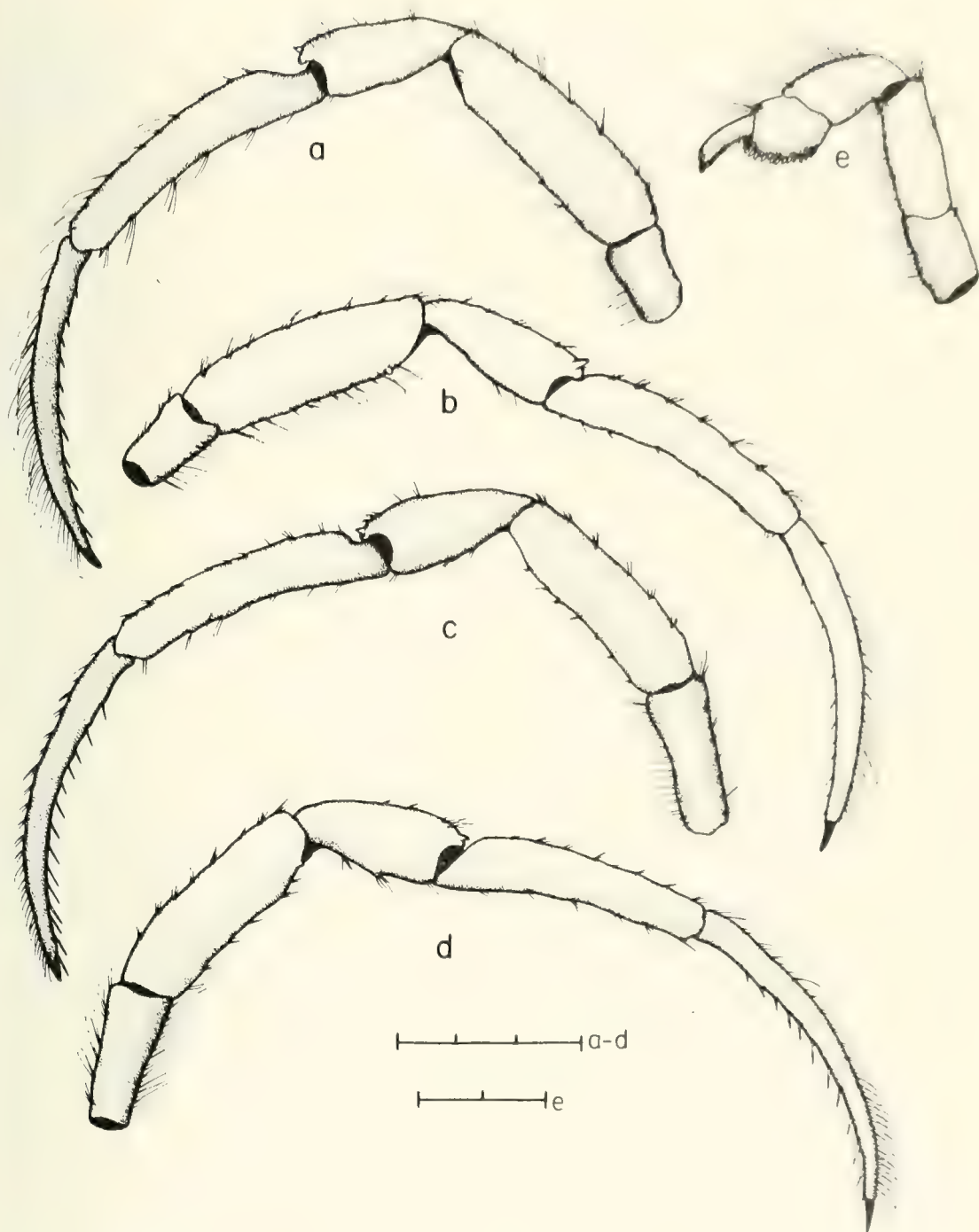


Figure 10. *Parapagurodes laurentae*, n. sp., paratype, ♂ (SL = 3.2 mm). "Velero III" sta. 1429-41, a,b, P₂: a, lateral view; b, mesial view.—c,d, P₃: c, lateral view; d, mesial view.—e, P₄, lateral view. Scales equal 3 mm (a-d) and 1 mm (e).

rarely slightly broader than long; anterolateral margins sloping; anterior margin between rostrum and lateral projections somewhat concave or occasionally straight; posterior margin truncate or roundly truncate; dorsal surface slightly inflated, convex, usually with few scattered tufts of short setae; anterolateral angle produced, blunt or with small spine or spinule. Rostrum moderately long, or less frequently, short, usually exceeding lateral projections, depressed distally; triangular, usually slender, occasionally moderately broad, frequently with weak median keel; terminating acutely or subacutely, often with small spine and few moderately long setae. Lateral projections obtusely triangular, unarmed or occasionally with submarginal spinule.

Ocular peduncles moderately short, one-half to two-thirds length of shield, stout; slightly inflated basally and with corneae dilated; dorsal surface with irregular row of tufts of short setae. Ocular acicles triangular or subtriangular, narrow or moderately broad, with dorsal surface frequently slightly concave; terminating subacutely with strong, submarginal spine; separated basally by one to one and one-half times basal width of one acicle.

Antennular peduncles moderately long, exceeding ocular peduncles by three-fourths to entire length of ultimate segment. Ultimate segment with one or two short setae on dorsal surface distally; penultimate segment often with few short setae; basal segment with small spine on dorsolateral margin, ventrodistal margin often with small spinule and tuft of setae.

Antennal peduncles moderately long, exceeding ocular peduncles by one-fourth to three-fourths length of ultimate segment; with supernumerary segmentation. Fifth segment unarmed, usually with few stiff setae or bristles dorsally and ventrally. Fourth segment unarmed, with few tufts of short setae. Third segment with strong spine at ventrodistal margin, partially obscured by tuft of setae. Second segment with dorsolateral distal angle produced, terminating in strong spine, dorsal surface and mesial margin occasionally with one or two small spines or spinules and tufts of short to long setae, lateral margin with scattered short setae; dorso-mesial distal angle with strong spine, mesial margin with short, stiff setae. First segment with small spine or spinule on lateral face distally; ventrodistal margin produced, with one to several spines laterally. Antennal acicle moderately long, slightly shorter than or equalling length of ocular peduncles, and usually exceeding proximal third of ultimate peduncular segment; terminating in strong, acute spine; dorsal surface and mesial margin with tufts of stiff setae. Antennal flagella long, equalling or exceeding tip of right cheliped; naked or with intermittent, short bristles.

Mandible without significant characters. Maxillule with proximal endite slightly tapered; endopodite with one bristle on moderately well-developed in-

ternal lobe, external lobe moderately well-developed, not recurved. Maxilla with endopodite long, exceeding scaphognathite in distal extension, slightly reflexed. First maxilliped with flagellum of exopodite short, slender. Second maxilliped with basis-ischium fusion incomplete. Third maxilliped with basis-ischium fusion incomplete; basis with one to three strong teeth; ischium with crista dentata well-developed, one accessory tooth; merus and carpus each with spine at dorsodistal margin. Sternite of mxp₃ with prominent spine and row of long setae on either side of midline.

Right cheliped usually long, moderately slender, particularly in large specimens; surfaces usually with scattered tufts of long, stiff setae. Dactyl moderately long, two-thirds to three-fourths length of palm, occasionally equalling or slightly exceeding length of palm; set at slightly oblique angle to palm; terminating in small, corneous claw, slightly overlapped by fixed finger; cutting edge with calcareous teeth on proximal one-half to two-thirds, replaced distally by row of small, corneous teeth; usually with prominent, longitudinal hiatus; dorsomesial margin with row of moderately strong, blunt, or, in small specimens, acute, tubular spines, dorsal surface slightly elevated in midline, usually with one or two strong, tubular spines and frequently short longitudinal row of small spines or tubercles not extending beyond proximal half; mesial and ventral surfaces unarmed. Palm usually elongate, one-half to two-thirds length of carpus, moderately slender, particularly in large specimens, somewhat inflated dorsoventrally; dorsal surface convex, with four or five, widely spaced, irregular rows of tubular spines, usually very prominent in large specimens, not extending beyond proximal half of fixed finger; dorso-mesial margin with row of moderately short spines, mesial face proximally produced into prominent shelf, marginally armed with strong, tubular spines, distally with irregular row of small spines or tubercles; dorsolateral margin with row of small spines, increasing in size and becoming tubular on fixed finger, lateral face usually unarmed; ventral surface with scattered small tubercles or spines. Carpus very elongate, considerably exceeding length of merus; dorsomesial margin with row of strong, slender spines, increasing in size distally, dorsal surface with row of moderately strong spines slightly mesial of midline extending from distal margin proximally two-thirds to three-fourths length of segment, rarely extending to proximal margin, and with usually short row of small spines laterad of midline, distal margin usually with one or two subacute spines; dorsolateral margin not delimited or with irregular row of small spines or spinulose protuberances, lateral face unarmed or slightly spinulose; ventrolateral margin with short row of small to moderately strong spines distally, ventral surface unarmed or with few low, occasionally spinulose protuberances; mesial face with scattered, often spinulose pro-



Figure 11. *Parapagurodes laurentae*, n. sp., a,b, d-g, paratype, ♂ (SL = 3.2 mm), "Velero III" sta. 1429-41: a, sternite, P₃; b, coxae and sternite P₃; d, telson; e, branchial lamella; f, antennular peduncle; g, antennal peduncle.—c, h-m, ♂ (SL = 3.4 mm), "Velero III" sta. 895-38: c, coxae and sternite, P₃—h-m, same, mouthparts (left internal face): h, mandible; i, maxillule; j, maxilla; k, mxp₁; l, mxp₂; m, mxp₃. Scales equal 0.5 mm (a,d,e) and 1 mm (b,c,f-m).

tubercles, ventromesial margin with irregular row of moderately strong spines, increasing in size distally. Merus subtriangular; dorsal surface with irregular rows of low, occasionally spinulose protuberances; mesial and lateral faces usually unarmed, ventromesial and ventrolateral margins each with single or double row of spines, strongest mesially. Ischium with row of small spines on ventromesial margin, mesial face often with prominent protuberance dorsally. Coxa unarmed.

Left cheliped moderately long, usually reaching to base of dactyl of right, slender; surfaces usually with tufts of long, stiff setae. Dactyl long, one and one-half to more than twice length of palm; cutting edge with row of small, corneous teeth; terminating in broad, corneous claw; often with slender, longitudinal hiatus; dorsal surface usually unarmed, occasionally with few, low, spinulose protuberances proximally. Palm moderately short, one-fourth to one-third length of carpus; dorsal surface convex, with irregular, single or double row of tubular spines, usually not extending onto fixed finger, dorsomesial margin with row of strong, tubular spines, becoming obsolete distally on fixed finger; dorsolateral margin not delimited or with irregular row of small spines or spinulose protuberances, lateral, mesial, and ventral surfaces unarmed. Carpus elongate, usually exceeding length of merus, subrectangular; dorsomesial and dorsolateral margins each with row of moderately strong or strong spines; mesial and lateral faces usually with few, scattered, low protuberances, ventromesial, and ventrolateral margins each with row of small spines, or less frequently with only few low protuberances. Merus subtriangular; dorsal surface with two irregular, longitudinal rows of low protuberances; mesial and lateral faces usually unarmed, or occasionally with few low protuberances, ventromesial and ventrolateral margins each with single or double row of moderately strong spines. Ischium with row of small spines on ventromesial margin. Coxa unarmed.

Second and third pereopods long, usually equalling or overreaching tip of right cheliped; dorsal and ventral surfaces usually with tufts of moderately long, stiff setae. Dactyls elongate or moderately elongate, equalling or somewhat exceeding length of propodi; in lateral view, curved ventrally; in dorsal view, usually straight; terminating in strong corneous claws; dorsal margins each with row of widely spaced, low protuberances; mesial and lateral faces unarmed; ventral margins each with row of strong, corneous spines, increasing in size distally. Propodi elongate, one and one-half to twice length of carpi; dorsal surfaces each usually with row of low protuberances; mesial and lateral faces unarmed; ventral margins each with one or two small, corneous spines or spinules distally. Carpi moderately short, two-thirds to three-fourths length of meri; dorsal surfaces each usually with small spine at distal margin; lateral and mesial faces unarmed; ventral

margins each frequently with small, occasionally spinulose protuberance. Meri laterally compressed; dorsal surfaces each with row of low, occasionally spinulose protuberances; lateral faces unarmed, mesial faces each with small spine on ventral margin distally; ventral margins usually with row of small spines (P_2) or unarmed (P_3). Ischia and coxae unarmed.

Fourth pereopods usually weakly subchelate, occasionally not subchelate. Dactyls with very small, preungual process on lateral face; propodal rasp with one to three rows of corneous scales.

Fifth pereopods chelate; coxae symmetrical.

Sternite of third pereopods subsemicircular; anterior margin with long, stiff setae.

Males with well developed, short sexual tube on right, occasionally with vas deferens of left slightly produced. No paired pleopods, unpaired pleopods, pl_2 to pl_4 , biramous, weakly developed, occasionally pleopods absent.

Females with paired gonopores; no paired pleopods, unpaired pleopods, pl_2 to pl_4 , with both rami moderately well-developed, or infrequently weakly developed; pl_5 usually rudimentary, occasionally absent.

Uropods asymmetrical. Telson with posterior lobes generally symmetrical; separated by very shallow median cleft; terminal margins concave or slightly oblique, each with row of very small spinules and one to four small spines at extrolateral angles, lateral margins with few short setae; anterior lobes unarmed, margins with long setae.

COLORATION.—Living color unknown. In preservative: Body and appendages straw-colored.

DISTRIBUTION.—Southern California, Channel Islands, to west coast of Baja California, Mexico; Gulf of California; 16 to 475 meters.

AFFINITIES.—Although *Parapagurodes laurentae* is most closely related to *P. makarovi*, its superficial resemblance to an undescribed species of *Pagurus* that has come to our attention, may cause mistakes in identification. In addition to the presence of sexual tubes in the males, the lack of spines on the distal portions of the dorsal surfaces of the dactyls of the chelipeds, the moderately long and relatively slender dactyls of the second and third pereopods, and the lack of regular setation on the articles of the antennal flagella are characters which distinguish *P. laurentae*.

ETYMOLOGY.—*Parapagurodes laurentae* is named in honor of Michèle de Saint Laurent, the French carcinologist who has contributed so greatly to pagurid systematics.

DISCUSSION.—As previously mentioned, both species of *Parapagurodes* were often found infested with *Stegophryxus* sp. The questionable inclusion of *Pagurus* [sp.] in the synonymy of *Parapagurodes laurentae* is based on the fact that this record of Menzies and Miller (1954) is

the only other report of this bopyrid genus from western North America. It is improbable that these authors would not have been able to recognize their pagurid host had it been *P. makarovi*, as this species has been well illustrated under the name *Parapagurus mertensii* (Rathbun, 1904, 1910; Schmitt, 1921; Makarov, 1938). In contrast, *Parapagurodes laurentae* is not only an undescribed species, but it does bear a strong, superficial resemblance to some species of *Pagurus*.

Key to the Species of *Parapagurodes*

- Palm of right cheliped with dorsal surface unarmed proximally, and with scattered small spinules or spinulose tubercles distally and on fixed finger. Palm of left cheliped with dorsal surface unarmed or with minute spinules *P. makarovi*, n. sp.
- Palm of right cheliped with dorsal surface armed proximally with four or five irregular rows of widely spaced, strong, tubular spines, not extending onto fixed finger. Palm of left cheliped with dorsal surface with single or double row of strong tubular spines *P. laurentae*, n. sp.

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COMPARATIVE STUDY OF THE CALCANEA OF MEMBERS OF THE URSIDAE AND PROCYONIDAE

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ABSTRACT: Calcanea of all of the bears and all but one genus of procyonids are compared and described. These calcanea indicate a close similarity of members of these two families. Some arrangement into subgroups can be made in each of the families. In the Ursidae, the calcanea of *Ursus maritimus*, *Tremarctos*, and *Helarctos* are similar; and those of *Ursus americanus*, *Ursus arctos*, *Selenarctos*, *Melursus*, and *Ailuropoda* are similar. In the Procyonidae, the calcanea of *Procyon* and *Nasua*, *Potos* and *Bassaricyon*, and *Ailurus* and *Bassariscus* are similar. The degree of development of the trochlear process and the proximal extension of the trochlear shelf is the major difference between members of the two families. Differences are also evident in the various articular surfaces and the greater tuberosity.

The relationship of members of the families Ursidae and Procyonidae seem to be close, at least on the same line of evolution as the Canidae. The disputed position of the giant panda is one indication of the close relationship of these two families. Some of the early workers (Raven, 1936; Gregory, 1936) conclude that the giant and lesser pandas are closely related based on soft anatomy, skull and dentition, and place both in a separate subfamily of the Procyonidae. Walker (1964) places the giant panda in the Procyonidae. Davis (1964), based on soft anatomy, and Leone and Wiens (1956), based on serology, place the giant panda in the family Ursidae. Simpson (1945) and Romer (1966) discuss the relationship of these two families to the Canidae. Stains (*in* Anderson and Jones, 1967) summarizes the morphological characteristics and taxonomy of these families.

Like studies of the teeth, skulls, myology, and blood, study of the calcanea of living procyonids and ursids of the world indicate these two families are closely related. The object of this paper is to point out the intra-family similarities and differences in the structure of calcanea of living members of these two families. There is no intent to imply evolutionary relationships simply because of the similarities or differences noted. A discussion of the features of the calcanea and a comparison of these features by genus within each family follows. The terminology follows that of Stains and Robinette (1970) and Stains (1959 and 1962) and is illustrated in figure 1. Measurements were taken in the manner illustrated in figure 2 and all are expressed in millimeters.

All genera and species of the family Ursidae were available for study. Because of the similarity to the calcanea of *Melursus*, *Ailuropoda melanoleuca* is included with the bears rather than the procyonids. Of the Procyonidae, *Nasua* was the only genus not available for study. Aside from island species of *Procyon* and *Nasua*, other questionable species not available were *Bassaricyon alleni* and *Bassariscus sumichrasti*.

CALCANEA OF MEMBERS OF THE FAMILY URSIDAE

Ursus maritimus—Polar Bear

In general, the calcanea of *Ursus maritimus* are larger than those of other bears. There is some overlap, especially in length of calcaneum, with *Ursus arctos* (Table 1). Only five of 28 specimens of *U. arctos* have calcanea with widths as great or greater than the bones of two immature specimens of the polar bear, and only one specimen of the brown bear has a heel bone as wide as one of five subadult and adult specimens of the polar bear. Proportionately, the width/length index of the calcaneum in the polar bear (Table 2, W/TL) is slightly larger than in the brown bear. These two bears can be distinguished most easily by the proximo-distal length of the trochlear process compared with the width of the calcaneum (Table 2, LTP/W). In the polar

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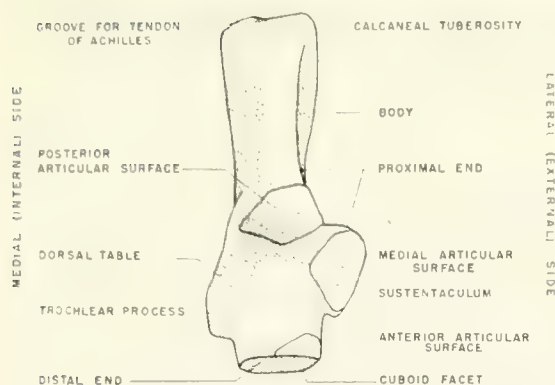


Figure 1. Dorsal view of generalized calcaneum of a carnivore.

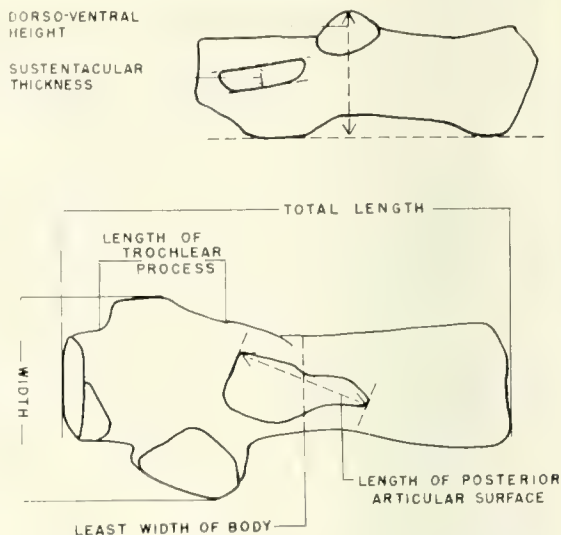


Figure 2. Measurements taken on the calcaneum.

bear this process is a smaller percentage of the width than in the brown bear.

The bear closest to the polar bear, in the form of the trochlear process, is *Tremarctos* (Fig. 3e) where the trochlear process extends outward as a continuation of the posterior articular surface. In *Ailuropoda* (Fig. 3j) the trochlear process is short as in the polar bear but is not a continuation of the posterior articular surface and has the development of a notch between the posterior articular surface

and the trochlear process (Fig. 3i). In other bears this process tends to go below to form a distinct shelf under the posterior articular surface. *Tremarctos* also is closest to the polar bear in an average width to length index (Table 2, W/TL). *Selenarctos* is next but has a distinct

TABLE 1. Measurements of the calcanea of members of the Ursidae.

*	No.	Total length (mm)		Width (mm)		LPAS (mm)	
		Range	Avg.	Range	Avg.	Range	Avg.
1	5	100.6-111.3	103.5	69.7-77.4	74.2	30.5-38.8	35.1
2	20	66.2-111.2	83.7	44.0-71.9	54.1	24.2-41.4	30.6
3	17	60.4- 75.6	66.5	33.5-46.1	41.1	17.5-25.1	22.0
4	14	58.1- 71.5	64.1	37.8-44.6	40.9	20.6-27.9	24.0
5	10	44.3- 67.9	60.4	30.2-46.3	40.2	16.8-25.6	21.5
6	5	55.1- 70.8	63.4	33.2-43.6	39.0	17.8-24.0	22.5
7	4	45.6- 52.8	49.8	30.6-35.1	33.6	18.1-20.6	19.7
8	1	50.1		32.0		17.8	

*	No.	ST (mm)		D-VH		LWB	
		Range	Avg.	Range	Avg.	Range	Avg.
1	5	17.5-22.2	19.6	50.4-57.6	53.9	21.1-25.3	23.2
2	20	12.3-24.1	16.3	34.0-57.6	43.4	12.6-23.1	17.4
3	17	7.2-12.9	11.7	30.5-37.4	34.5	10.6-14.9	13.4
4	14	8.4-12.2	10.2	27.0-34.0	29.6	10.6-12.7	11.6
5	10	7.0-11.3	9.7	20.9-35.9	28.7	8.5-13.2	10.6
6	5	6.8-11.8	9.7	24.5-35.8	30.7	10.8-13.7	11.9
7	4	8.7- 9.8	9.3	22.0-26.4	24.3	7.3- 8.4	7.7
8	1	6.5		21.1		8.0	

* 1, *Ursus maritimus*, 2, *U. arctos*, 3, *U. americanus*, 4, *Ailuropoda melanoleuca*, 5, *Selenarctos thibetanus*, 6, *Melursus ursinus*, 7, *Tremarctos ornatus*, 8, *Helarctos malayanus*, LPAS length of posterior articular surface, ST sustentacular thickness, D-VH dorso-ventral height, LWB least width of body (see Fig. 2 for measurement procedures).

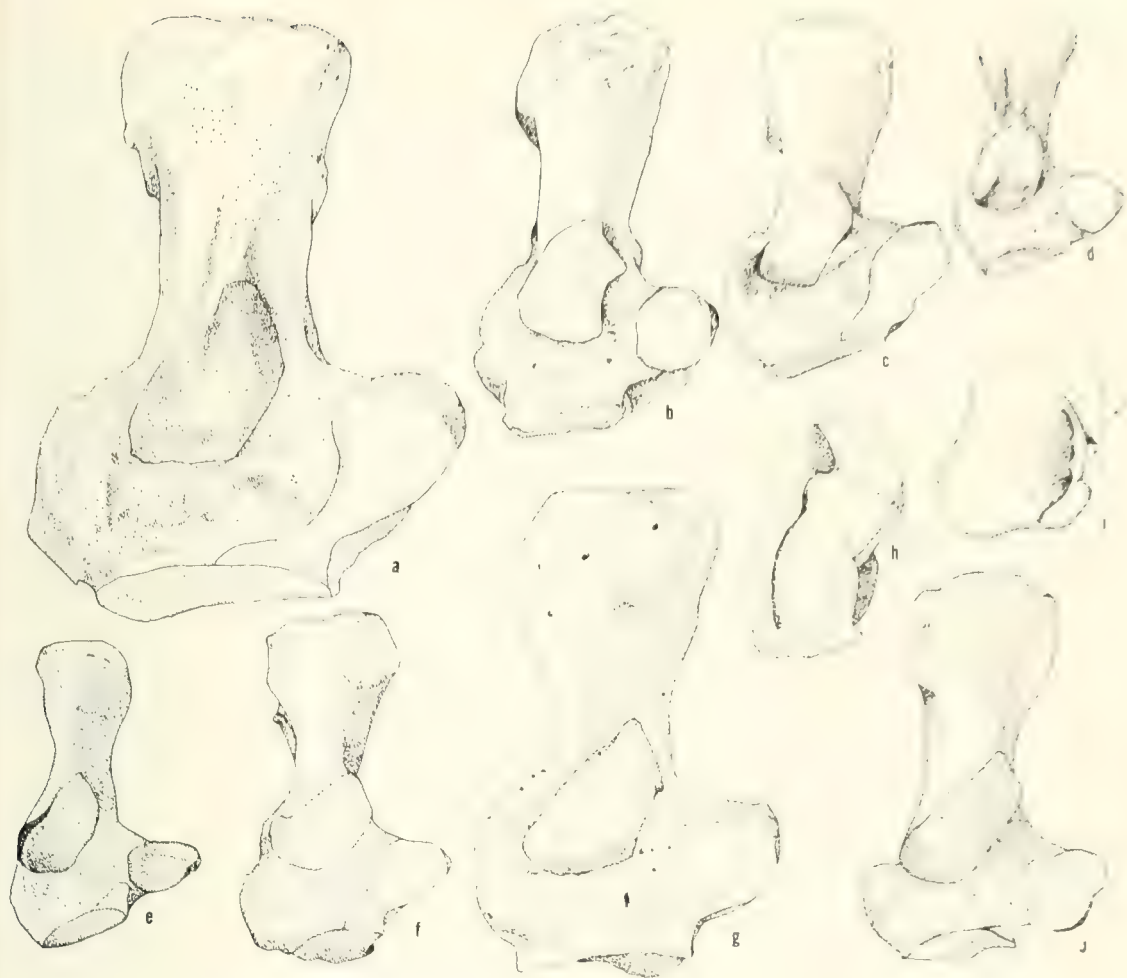


Figure 3. Right calcaneae of members of the Ursidae. a, *Ursus maritimus*; b, *U. americanus*; c, *Melursus ursinus*; d, *Helarctos malayanus*; e, *Tremarctos ornatus*; f, *Selenarctos thibetanus*; g, *U. arctos*; h, showing distance from outer edge of trochlear shelf to center of inner edge of posterior articular surface in *Ursus americanus*; i, notch between posterior articular surface and trochlear process in *Ailuropoda melanoleuca*; j, *Ailuropoda melanoleuca*.

shelf formed by the trochlear process (Fig. 3f).

Specimens examined: AMNH 14058 (yg), 15686-7 (yg), 22885, 75244-5, 100039 (AMNH 22885 illustrated, Fig. 3a).

Ursus arctos—Brown Bear

The calcaneum of *Ursus arctos* is extremely variable in size within and between different age groups. In 20 adults the range is from 66.2-111.2 mm (avg. 83.7) in length, and two young (greater tuberosity not completely ossified) range from 67.9-75.5 mm. In width of calcaneae, adults range from 44.0-71.9 (avg. 54.1 mm), and six

young range from 43.6-53.1 (avg. 48.4 mm). The larger specimens come from Alaska, the smaller calcaneae come from brown bears of western United States and are less than 85 mm in length and less than 55 mm in width.

The brown bear (Fig. 3g) can be distinguished from the polar bear (Fig. 3a) because of the greater proximal expansion of the trochlear process in the brown bear. In *Ursus maritimus*, the proximo-distal length of the trochlear process is from 40.8-48.1 (avg. 44.7) percent of the width and in the brown bear, 51.2-69.8 (avg. 59.6) percent. This ratio will separate both young and adult polar bears from brown bears.

TABLE 2. Indices for calcanea of members of the Ursidae.

Species	W/TL*		LTP/W*		D-VH/TL*		LWB/D-VH*	
	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
<i>Ursus</i>								
<i>maritimus</i>	68-75	72	41-48	45	49-56	52	39-45	43
<i>Ursus</i>								
<i>arctos</i>	60-73	65	51-70	60	48-58	53	33-50	40
<i>Ursus</i>								
<i>americanus</i>	55-67	62	55-77	68	49-56	52	31-44	39
<i>Ailuropoda</i>								
<i>melanoleuca</i>	59-70	64	35-44	40	44-51	46	36-43	39
<i>Selenarctos</i>								
<i>thibetanus</i>	61-70	67	45-69	58	44-54	47	33-41	37
<i>Melursus</i>								
<i>ursinus</i>	60-62	62	59-69	64	45-51	49	36-44	39
<i>Tremarctos</i>								
<i>ornatus</i>	66-70	68	28-32	31	47-52	49	28-35	32
<i>Helarctos</i>								
<i>malayanus</i>	—	64	—	51	—	42	—	38

* W/TL, width divided by total length; LTP/W, length of trochlear process divided by width; D-VH/TL, dorso-ventral height divided by total length; LWB/D-VH, least width of body divided by dorso-ventral height (See Fig. 2 for measurement procedures).

The calcaneum of the brown bear can be distinguished from the black bear (*Ursus americanus*, Fig. 3b) by the anterior articular surface being continuous with and broadly connected with the medial articular surface. In only four of 26 specimens of the brown bear are the two surfaces separate; in no case is the anterior articular surface absent. In the calcanea of 20 black bears, 10 lack the anterior articular surface and 10 have a small anterior articular surface, usually separate from the medial articular surface, although the two surfaces may be joined by a narrow band. There seems to be no relationship between age of the bear and the amount of juncture of the two surfaces in the grizzly although in all the young the two surfaces are joined.

Regardless of age, the best calcaneal character for the separation of the brown and black bears is in the size of the posterior articular surface. In the bones of the brown bear, the length of this surface is greater, and in the black bear is shorter (Table 1, LPAS). Using this characteristic, only two adults, of 26 young and adult brown bears, fall within the upper limits of the range of the black bear, and only one of 17 adult black bears falls within the lower limits of the range of the brown bear.

Except for size, the calcaneum of *Selenarctos* (Fig. 3f) seems to be the most difficult to distinguish from *Ursus arctos*. The indices of width to total length are the closest of all the bears.

If the calcanea of the larger *Selenarctos* are compared with those of small brown bears, the length of the posterior articular surface, total length, width of the bones, and the proportion of the length of the trochlear process to the width of the calcanea are closest in these two species.

The thickness of the sustentaculum does separate the calcanea of *Selenarctos* from *U. arctos* (Table 1, ST). *Ursus arctos* also can be distinguished from *Melursus* and *Ailuropoda* on the basis of the thickness of the sustentaculum. In addition, the length of the posterior articular surface in *Melursus* is less (Table 1, LPAS). The posterior articular surface also tends to be less in *Ailuropoda*. The calcanea of both *Melursus* (Fig. 3c) and *Ailuropoda* (Fig. 3j) have a distinct notch at the outer distal corner of the posterior articular surface (Fig. 3i), a characteristic which separates the bones of these genera from those of all other bears.

The calcaneum of the smallest specimen of *Ursus arctos* is greater in length and width than any specimens examined of *Tremarctos* or *Helarctos*. In addition, the heel bones of *Tremarctos* (Fig. 3e) and *Helarctos* (Fig. 3d) have a distinct rolling of the outer edge of the posterior articular surface which *U. arctos* lacks.

Specimens examined: AMNH 3767 (yg), 14054, 35590, 35887, 45150, 62553-4, 70163, 70330, 70448, 73694, 73696-7 (both yg), 125407, 129379 (yg), 135502, 149805, USNM

9483 (yg), 12322, 21337 (yg), 123386, 174950, 199252, 252303, 283624 (yg), 292072, 301690 (USNM 123386 illustrated, Fig. 3g).

Ursus americanus—Black Bear

The calcaneum of the black bear is much smaller than that of the polar bear and no overlap in measurements exists. Differences in the calcanea of the black and brown bears have been discussed under *Ursus arctos*.

As is indicated in table 1, one difference between *U. americanus* and *Selenarctos* is in the length of the calcaneum. As will be discussed later under *Selenarctos*, there seem to be two distinct groups of calcanea; the adults with the smaller calcanea of these two groups fall below the size of the smallest adult black bears, but the group with larger calcanea (length 66.1–67.9 mm; width 40.6–46.3 mm) falls within the size of the black bears (Table 1).

One measurement that separates adult *U. americanus* from all *Selenarctos* is the distance of the outer edge of the trochlear shelf to the center of the inner edge of the posterior articular surface (see Fig. 3h). In bones of the adult black bear, this distance ranges from 11.1–14.2 (avg. 12.7 mm) and in adult *Selenarctos* from 5.9–10.8 (avg. 8.4 mm) in five specimens. In five of 10 adult specimens of *Selenarctos*, the shelf of the trochlear process does not extend proximal enough to obtain a measurement. This is true of all three of the specimens of young animals. Seven young and very young black bears tend to have less development of the trochlear shelf producing measurements within the range of the adult *Selenarctos* (range 5.7–13.9, avg. 11.9 mm).

Ursus americanus seems to be most like *Melursus* in various calcaneal characteristics and indices (see Table 2). One character separates all *Melursus* (five adult specimens) from all *U. americanus* (24 adult and young specimens). The calcanea of *Melursus* (Fig. 3c) have a distinct notch (Fig. 3i) on the outer distal corner of the posterior articular surface as does *Ailuropoda*. In *Ursus* (Fig. 3b), the posterior articular surface blends into the trochlear process on the distal part of the calcaneum.

The calcanea of *Tremarctos* (Fig. 3e) differ from those of *U. americanus* in the absence of a trochlear shelf, and *Helarctos* (Fig. 3d) differs in the extensive rolling of the outer edge of the posterior articular surface. In addition, both

Tremarctos and *Helarctos* are smaller than adult black bears. The expanded medial and posterior articular surfaces, the shorter trochlear process and the notched posterior articular surface separate *Ailuropoda* (Fig. 3j) from the black bear.

Specimens examined: AMNH 24157, 35046, 45149, 90321 (yg), 90333 (yg), 90334, 98950, 100125, 120843, 128521, 131829, 131830 (yg), 149894 (yg), 164283, 164284 (yg); USNM 49664 (yg), 220264 (yg), 240613, 255072, 260642, 269812, 283630, 302901, 303193 (USNM 255072 illustrated, Fig. 3b).

Ailuropoda melanoleuca—Giant Panda

The giant panda possesses a calcaneum similar to those of bears in most respects. The trochlear process is a prominent projection on the calcanea of *Ailuropoda* (Fig. 3j) and ursids but is knob-like and small in most procyonids. However, it does not form a shelf below the posterior articular surface in *Ailuropoda* as it does in most bears. *Tremarctos* (Fig. 3e) is similar to *Ailuropoda* in this respect. The trochlear process is not grooved either in the giant panda or in the ursids. It is grooved in all procyonids except for some individuals of *Procyon lotor* (absent in eight of 17 specimens, faintly grooved in the remaining nine). The proximo-distal length of the trochlear process is about one-fourth the total length of the calcaneum in *Ailuropoda* and *Tremarctos*; it is longer in other bears.

The calcaneal width-total length index (Table 2) of *Ailuropoda* lies within the range exhibited by the ursids, and is greater than that found in most procyonids. This index reflects the relative larger size of the trochlear process of the giant panda and the ursids.

The most distinct differences observed between the calcanea of ursids and *Ailuropoda* involve the posterior and medial articular surfaces. These two surfaces are raised higher above the bulk of the calcaneum in the giant panda than in the bears. The posterior articular surface in the giant panda forms a well-developed ledge because of its position high above the body of the calcaneum; this ledge is absent in the calcanea of ursids. The outer distal corner of the posterior articular surface forms a notch or groove in the calcaneum of *Ailuropoda* (Fig. 3j) and is similar to that in the calcaneum of *Melursus* (Fig. 3c). The posterior articular surface is longer com-

pared to width in *Ailuropoda* than in the bears and is less curved (flatter). This surface is sigmoid in the calcanea of most procyonids except *Potos* and *Nasua nasua*.

Unlike other members of the Procyonidae and Ursidae, the medial articular surface in *Ailuropoda* is expanded to the extent that the bulk of the sustentaculum is hidden when viewed from the dorsal aspect. In addition, a prominent notch is formed between the medial and anterior articular surfaces. This notch is present in *Melursus* (Fig. 3c), and *Tremarctos* (Fig. 3e) but tends to be obscured in these bears by the ventral expansion of the sustentaculum. Such a notch is not present in procyonids.

The anterior articular surface of the calcanea in *Ailuropoda* varies from absent (six specimens), to a minute triangular articulation entirely separated from the medial articular surface (10 specimens), to a condition where the two surfaces tend to be continuous (two specimens). This variation in the anterior articular surface is similar to the variation found in *Ursus americanus* (Fig. 3b). In all procyonids the anterior articular surface, when present, is usually minute and is never continuous with the medial articular surface, although it is joined by a small waist in eight of 18 specimens of the genus *Procyon*.

In general, the sustentaculum of *Ailuropoda* and the ursids is lower in position (more toward the cuboid surface) than in procyonids. The giant panda and the ursids lack the notch on the ventral side of the cuboid surface which is characteristic of procyonids.

Of the species of bears, the calcanea of *Ailuropoda* resemble most closely those of *Melursus* in shape of the greater tuberosity, the notch at the distal corner of the posterior articular surface, the notch between the medial and anterior articular surfaces, and many of the indices. Davis (1964) compares the calcanea of *Ailuropoda* with only the genus *Ursus* and does not go into great detail.

Specimens examined: USNM 258423, 258425, 258834 (yg), 258835-6, 258838, 258644, 258984 (yg), 259027-9, 259075, 259078 (yg), 259400 (yg), 259401-3 (USNM 258644 illustrated, Fig. 3j).

Selenarctos thibetanus—Asiatic Black Bear

There seems to be at least two, and perhaps three, distinct sizes of calcanea within *Selenarctos*

with no relationship to sex or age of the animals. The largest group (six specimens) has calcanea which range in length from 66.1 to 67.9 mm with the young of this group lacking the cap of the calcaneal tuberosity and still being 61.6 mm long. In addition, two of the adults measuring 66.6 to 67.0 mm still have traces of the symphysis of the calcaneal tuberosity, an indication that they probably are subadults. Seven adult specimens of the smaller group range in length from 44.3-59.6 mm with two of the adults being extremely small (44.3 and 50.4 mm). The two young of this group possess caps and measure 48.6 and 52.4 mm. Perhaps this smaller group is composed of two subgroups.

Both the larger and smaller groups are represented by both sexes and both groups have a preponderance of specimens obtained from zoos, although one from the group with large calcanea came from Japan and one from northern Burma; one of the small group also came from the Himalaya Mountains. If these localities are accurate, there simply may be a tremendous amount of variation similar to that found in *Ursus arctos*. Such distinction in size usually is an indication of species differences in the calcanea of most mammals. Thus there seem to be two, and perhaps three, distinct species present. The effect of living as caged animals may be the explanation of such variation, although in most caged animals the effect usually is rugoseness of the bone as is obvious in USNM 221064, a zoo specimen at least 15 years old.

The differences between the calcanea of *Selenarctos* and *Ursus maritimus*, *U. arctos*, and *U. americanus* have been discussed. *Selenarctos* (Fig. 3f) differs from *Melursus* (Fig. 3c) and *Ailuropoda* (Fig. 3j) in lacking the notch at the outer distal corner of the posterior articular surface (Fig. 3i). The calcaneum of *Selenarctos* tends to be wider than long when compared to *Melursus* (see the width-length indices in Table 2). The trochlear process in *Selenarctos* is not as well-developed as in *Melursus*.

Selenarctos differs from *Tremarctos* and *Ailuropoda* in having a much longer trochlear process (Table 2) compared to the width of the bone; *Tremarctos* (Fig. 3e) and *Ailuropoda* (Fig. 3j) lacking the development of a trochlear shelf.

Specimens examined: AMNH 23086, 35016, 35496, 70094 (yg), 70320, 80248, 90184 (yg), 100396 (2 animals same number), 114544 (yg),

119476, 171285; USNM 221064 (AMNH 70320 illustrated, Fig. 3f).

Melursus ursinus—Sloth Bear

The heel bone of *Melursus* (Fig. 3c) can be distinguished from all bears except *Ailuropoda* (Fig. 3j) in having a distinct notch located at the outer distal corner of the posterior articular surface (Fig. 3i). The length of the trochlear process divided by the width of the calcaneum separates all specimens of *Melursus* from *Ailuropoda* (Table 2). In general shape and expansion of the trochlear process, the calcaneum of *Melursus* is similar to *Ursus americanus* (Fig. 3b).

Specimens examined: AMNH 22720, 22896 (malformed), 35602, 35898, 54464–5 (AMNH 54464 illustrated, Fig. 3c).

Tremarctos ornatus—Spectacled Bear

The similarities of *Tremarctos* to *Ursus maritimus* have been discussed. All members of the genera *Ursus*, *Melursus*, and *Ailuropoda* have longer calcanea than the largest *Tremarctos* examined. *Tremarctos* can be separated from all of the bears on the basis of the ratio of the length of the trochlear process to the width of the calcaneum (Table 2, LTP/W). This index is less than that of other bears, *Ailuropoda* being closest. In overall size, the calcaneum of *Helarctos* is closest to *Tremarctos*.

Specimens examined: AMNH 35480, 70164, 100010, 194309 (AMNH 70164 illustrated, Fig. 3e).

Helarctos malayanus—Malayan Sun Bear

Only one specimen of the sun bear was available for examination. The calcaneum differs from the calcanea of all other bears in having the posterior articular surface prominently rolled over on the outer edge (Fig. 3d). There is a slight trochlear shelf present. The cuboid surface is at a great angle with the long axis of the bone. A flat groove leads from the proximal end of the posterior articular surface toward the greater tuberosity; this groove was not noted in other bears. A small anterior articular surface is present.

Specimens examined and illustrated: AMNH 70089, Fig. 3d.

CALCANEAL OF MEMBERS OF THE FAMILY PROCYONIDAE

Procyon lotor—Raccoon

The calcanea of members of the genus *Procyon* lack a distinct knob on the trochlear process (Fig. 4a and b). The trochlear process tends to be broad, originating close to the cuboid surface and gently sloping from the point where the knob is commonly present on other procyonids, to a point below and beyond the posterior articular surface. In this feature, the calcanea of *Nasua narica* (Fig. 4e) and *Bassaricyon gabbi* (Fig. 4d) most nearly resemble *Procyon*.

The heel bones of the two species of *Procyon* seem to differ in size (*P. cancrivorus* being larger) and in length of the posterior articular surface (*P. cancrivorus* being longer). In addition, the trochlear process of *P. lotor* has a less distinct groove, the dorsal edge of the cuboid facet in *P. lotor* has a distinct point, and there is an addition of another surface alongside the anterior articular surface (between this surface and the cuboid facet) in *P. cancrivorus* (Fig. 4b).

Procyon differs from *Nasua narica* (Fig. 4e) in that the medial articular surface is not folded over the proximal edge of the sustentaculum. The distal edge of the trochlear process is almost even with the cuboid surface in *Procyon*. In both species of *Nasua* (Fig. 4e and f), the distal edge of the trochlear process originates more proximally than in *Procyon*.

The calcanea of *Procyon* are much longer than those of *Bassaricyon* (Table 3, TL). In addition, *Bassaricyon* is similar to *Nasua* in the position of the distal edge of the trochlear process.

The tuber, or body, leading to the calcaneal tuberosity is more robust in *Procyon* than *Potos*. the cuboid facet is not turned dorsally in *Procyon* as in *Potos* (Fig. 4c), the medial articular surface is round in *Procyon* but is tear-shaped and wider than long in *Potos*, and the posterior articular surface is strongly sigmoid in *Procyon* but in *Potos* tends to form a smooth curve.

The distinct knob-like trochlear process of *Bassariscus* (Fig. 4h) and *Ailurus* (Fig. 4g) distinguishes the calcanea of these genera from *Procyon* (Fig. 4a and b).

Specimens examined: USNM 575, 1386, 21136 (yg), 144069, 187907, 22243, 256028–30 (all young), 256031, 256057 (yg), 259130–1 (both

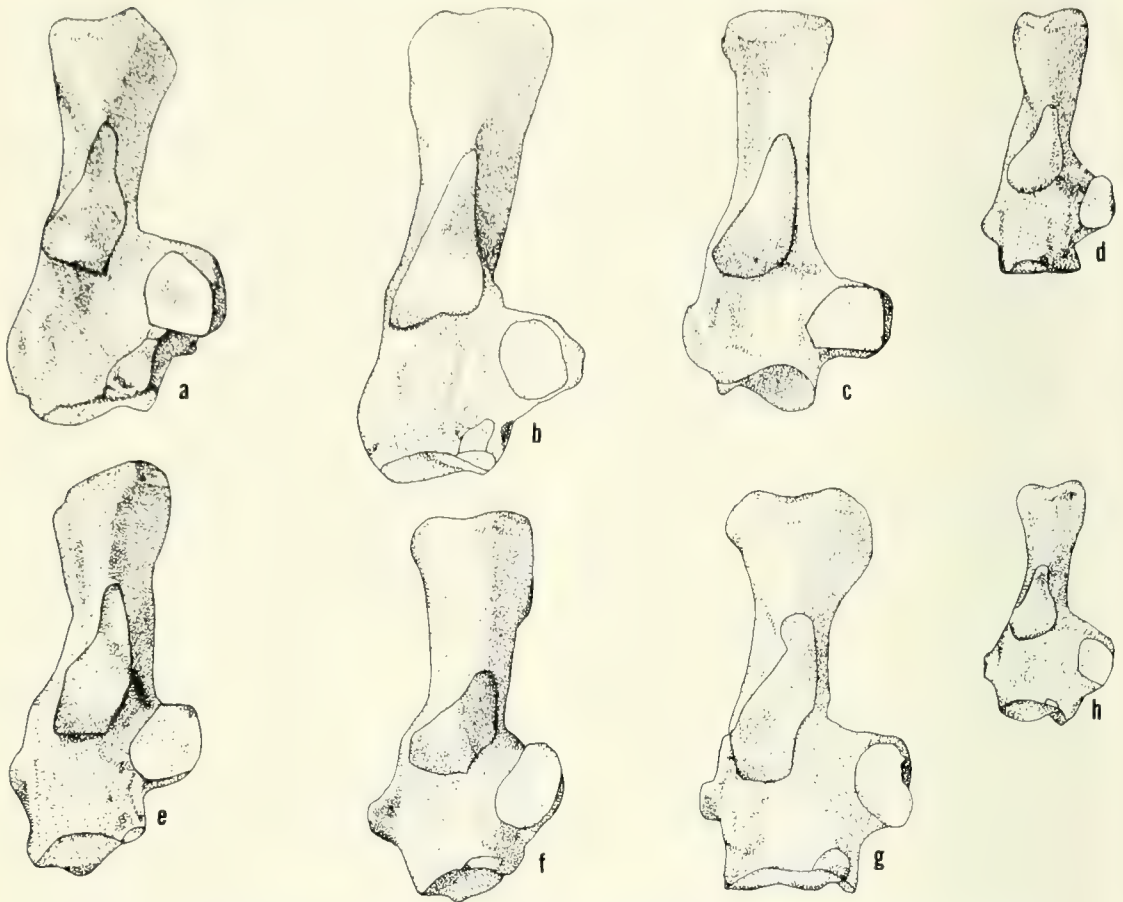


Figure 4. Right calcanea of members of the Procyonidae. a, *Procyon lotor*; b, *P. cancrivorus*; c, *Potos flavus*; d, *Bassaricyon gabbi*; e, *Nasua narica*; f, *N. nasua*; g, *Ailurus fulgens*; h, *Bassariscus astutus*.

young), 259132, 259137, 271097 (USNM 271097 illustrated, Fig. 4a).

Procyon cancrivorus—Crab-eating Raccoon

Comparison and characteristics of *Procyon cancrivorus* have been made under *Procyon lotor*. The calcaneum of the crab-eating raccoon tends to be larger than that of the common raccoon but otherwise is not too different.

Specimens examined: USNM 6949, 49718 (USNM 49718 illustrated, Fig. 4b).

Potos flavus—Kinkajou

In general, the posterior articular surface of the calcaneum of *Potos* is long, narrow, and practically in line or parallel with the body leading to the calcaneal tuberosity (Fig. 4c). In all other

procyonids, this surface tends to be broader and at more of an angle to the body of the bone. The trochlear process is located proximally in *Potos* near the distal edge of the posterior articular surface. In some specimens this process is poorly developed and virtually absent.

Differences between the bones of *Procyon* and *Potos* have been discussed. The extreme dorsal turning of the cuboid surface and the formation of a tear-shaped medial articular surface which is wider than long, separate *Potos* from the remaining procyonids.

The procyonid most closely resembling *Potos* in general features of the calcaneum is *Bassaricyon* (Fig. 4d). The difference listed above, as well as overall size (Table 3), will distinguish the two easily.

Specimens examined: AMNH 14073, 35192, 35352, 35434–5, 35766, 35916 (yg), 42302,

TABLE 3. Measurements of the calcanea of members of the Procyonidae.

		Total length (mm)		Width (mm)		LPAS (mm)		D-VH		LWB	
№	No.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
1	2	32.2–36.1	34.2	15.0–17.7	16.4	13.5–15.0	14.8	13.3–15.8	14.6	5.8–6.6	6.2
2	9	24.7–31.3	27.3	12.3–15.7	11.8	8.4–11.4	10.0	9.8–13.5	11.1	3.5–5.3	4.5
3	15	21.0–27.5	24.0	9.7–13.3	12.1	8.0– 9.2	8.5	7.6–10.1	8.5	2.6–3.6	3.1
4	10	23.7–29.7	27.3	12.1–16.1	14.2	8.8–11.3	10.2	8.9–10.8	10.1	3.3–5.8	4.8
5	4	26.0–27.7	26.8	13.3–18.1	14.8	8.0– 9.0	8.5	10.2–10.6	10.4	3.9–4.2	4.0
6	12	24.3–31.1	27.1	12.3–16.8	14.8	9.4–11.9	10.8	9.5–12.8	11.4	3.0–4.5	3.7
7	2	17.9–18.4	18.2	9.1– 9.2	9.2	6.1– 6.3	6.2	6.8– 7.1	7.0	2.5–2.6	2.6
8	10	14.0–17.1	15.8	7.2– 9.8	8.7	5.6– 6.4	5.9	5.8– 6.6	6.2	2.1–2.8	2.5

* 1, *Procyon cancrivorus*, 2, *Procyon lotor*, 3, *Potos flavus*, 4, *Nasua narica*, 5, *N. nasua*, 6, *Ailurus fulgens*, 7, *Bassaricyon gabbi*, 8, *Bassariscus astutus*; see Table 1 and Fig. 2 for measurements taken.

48216, 80223 (yg); USNM 49943, 241106, 241181, 255123, 257352, 258316; KU 68059 (yg), 69058 (USNM 258316 illustrated, Fig. 4c).

Bassaricyon gabbi—Olingo

On the basis of the trochlear process, *Bassaricyon gabbi* (Fig. 4d) is in the intermediate position between a broad, gently sloping condition and a distinct knob-like process. Other than *Bassariscus*, *Bassaricyon* possesses the smallest calcaneum. There is no overlap in size ranges with the larger species (Table 3). There is a slight tendency for the posterior articular surface to be sigmoid. The proximal edge of the medial articular surface is folded over the sustentaculum (true of the calcanea of all procyonids except *Procyon* and *Potos*).

The anterior articular surface is poorly developed, as in *Potos*, and could be listed as absent. In most characteristics, the calcaneum of *Bassaricyon* (Fig. 4d) resembles *Potos* (Fig. 4c).

Specimens examined: USNM 305748-9 (USNM 305748 illustrated, Fig. 4d).

Nasua nasua—Red Coati

The calcaneum of *Nasua* is intermediate in procyonid characteristics. The two species examined (*N. nasua*, Fig. 4f, from South America and *N. narica*, Fig. 4e, from Central and North America) differ in the ratio of the length of the posterior articular surface to the total length (Table 4, LPAS/TL). The posterior articular surface tends to be more sigmoid in *N. narica*, and more a smoothly curved surface in *N. nasua*. The groove on the edge of the trochlear process tends to be more distinct in *N. narica*. *Nasua narica* has a more conspicuous groove on

the outer surface of the body, below and proximal to the posterior articular surface. The trochlear process tends to be more knob-like in *Nasua nasua* than in *N. narica*. Most of the above characteristics are a matter of degree, but there was no difficulty in separating the specimens available. Perhaps specimens from northern South America would be intermediate between the two groups (species) examined, indicating a single species. Since specimens from the intermediate region are not available, the differences noted are of enough magnitude to regard these individuals as members of two different species.

More specific comparisons of the calcanea of *Nasua* have been discussed under the genera *Procyon* and *Potos*. *Ailurus* (Fig. 4g) and *Bassariscus* (Fig. 4h) tend to have smaller and more distinct knob-like trochlear processes and a tuberosity which tends to flare out and become more distinct from the body. The heel bones of *Nasua* differ from *Bassaricyon* (Fig. 4d) in being of larger size, having a longer trochlear process in relation to total length, and in the presence of a minute additional articular surface next to the anterior articular surface (this additional surface also is present on the calcaneum of *Procyon cancrivorus*).

Specimens examined: AMNH 347, 42699, 100448 (yg); USNM 49644, 238671 (yg), 270366 (AMNH 347 illustrated, Fig. 4f).

Nasua narica—White-nosed Coati

Comparisons of *Nasua narica* with other species of procyonids and with *Nasua nasua* were made previously under a discussion of red coati.

Specimens examined: AMNH 5904, 18688, 35656, 70078; USNM 983, 21982 (yg), 22810.

TABLE 4. Indices for calcanea of members of the Procyonidae.

Species	W/TL	Index*	LTP/W	Index*	D-VH/TL*		LWB/D-VH*		LPAS/TL*	
	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.	Range	Avg.
<i>Procyon</i>										
<i>cancrivorus</i>	46-49	48	77-86	82	41-44	43	42-44	43	—	42
<i>Procyon lotor</i>	44-56	50	67-92	76	39-44	42	36-46	41	34-39	37
<i>Potos flavus</i>	47-56	51	46-66	58	32-38	35	32-46	36	33-39	38
<i>Nasua narica</i>	48-54	52	54-71	65	35-40	37	37-54	47	34-41	38
<i>Nasua nasua</i>	48-54	51	61-77	67	37-40	39	37-40	39	30-34	32
<i>Ailurus</i>										
<i>fulgens</i>	50-59	54	33-49	42	39-46	42	27-36	32	35-44	40
<i>Bassaricyon</i>										
<i>gabbi</i>	50-51	51	52-53	53	39	39	35-38	37	—	34
<i>Bassariscus</i>										
<i>astutus</i>	51-58	55	47-57	52	37-41	39	36-45	41	35-40	38

* See Table 2 and Fig. 2 for measurements taken.

257314, 271136, KU 63118, 68056 (USNM 257314 illustrated, Fig. 4e).

Ailurus fulgens—Lesser Panda

Ailurus fulgens (Fig. 4g) and *Bassariscus astutus* (Fig. 4h) have the most knob-like trochlear processes of all the procyonids. In addition, this process begins higher above the cuboid surface. The distal edge of the trochlear process is even with the distal edge of the medial articular surface. In all other procyonids the distal edge of the trochlear process is distal (closer to the cuboid surface) to the medial articular surface.

The calcaneum of *Ailurus* is much larger than that of *Bassariscus* and tends to have a greater flaring of the tuberosity.

The calcaneal relationships of *Ailurus* to other procyonids have been discussed under previous genera.

Specimens examined: AMNH 119474, 119675, 146778; USNM 252087, 252091, 252146, 256098, 258051, 258350, 258850, 305770-1 (USNM 252146 illustrated, Fig. 4g).

Bassariscus astutus—Ring-tailed Cat

The calcaneum of *Bassariscus astutus* is the smallest of all the procyonids. In almost all features, the calcaneum of *Bassariscus* is a miniature of *Ailurus fulgens* (Fig. 4g).

Specimens examined: AMNH 35909, 100094, 135964-6, 137029-30; USNM 1619, 49934; KU 58649 (AMNH 35909 illustrated, Fig. 4h).

DISCUSSION

The calcanea of bears are quite similar (Fig. 3, Tables 1 and 2). However, there are differences which make it possible to identify each species. Bears have a calcaneum with an obvious trochlear process. This process is expanded into a prominent trochlear shelf which in most cases (except *Tremarctos* and *Ailuropoda*) extends to below the posterior articular surface. The posterior articular surface is smooth, never sigmoid. The medial articular surface tends to be rolled over the proximal edge of the sustentaculum. The amount of rolling is extremely variable within all species with the angle of curl being from slight to 90°. There is a tendency for the medial and anterior articular surfaces to be joined; this is especially true of the bones of larger bears (*U. arctos*, *U. maritimus*, and *Melursus*). In the others, the two surfaces may or may not be joined, but seldom broadly. The sustentaculum varies in thickness in the different bears. Some question the generic separation of *Tremarctos* from *Ursus* and place *Selenarctos* midway between *Tremarctos* and *Ursus* (Simpson, 1945). The placement of *Thalarchos* (the polar bear) and *Euarctos* (the black bear) in the genus *Ursus* is generally accepted today (see Stains, in Anderson and Jones, 1967). The generic separation of *Melursus* and *Ursus* is adopted by all authors (Simpson, 1945). Studies of the calcanea indicate a close similarity between *Ursus maritimus* and *Tremarctos*, between *Ursus americanus* and *Melursus*, and between *Ursus arctos* and *Selenarctos*.

The calcanea of all procyonids are basically similar in appearance to those of bears; both groups having calcanea with an obvious trochlear process. There is less massive development of the trochlear process in procyonids thus a smaller ratio of width of the calcaneum to length (Tables 4 and 2, W/TL). There is little extension of the shelf of the trochlear process up to or beyond the distal edge of the posterior articular surface in the procyonids as in the bears. This process forms a distinct knob in some procyonids. Size and location of the trochlear process are the most obvious differences between various members of the Procyonidae (Fig. 4, Table 3).

In most procyonids, except *Potos* and *Nasua nasua*, the posterior articular surface is sigmoid in shape. In *Bassaricyon* it tends to be slightly sigmoid. In no case is there a tendency for the surface to be rolled as in some ursids. The cuboid surface tends to be half-moon in shape caused by a notch on the ventro-lateral edge of the cuboid surface and tends to slope dorso-ventrally, especially in *Potos* (Fig. 4c). The anterior surface may be present, minute, or absent but seldom joined to the medial articular surface in the procyonids.

CONCLUSIONS

On the basis of the characteristics of the calcaneum, bears can, in general, be grouped according to similarities and differences. *Ursus maritimus* and *Tremarctos* are most similar in general shapes and proportions of the heel bone. *Ursus americanus* and *Melursus* likewise are similar to each other. *Ursus arctos*, *Selenarctos*, and *Ailuropoda* seem closer to the *U. americanus-Melursus* group and *Helarctos* seems closer to the *Ursus maritimus-Tremarctos* group.

The trochlear process in procyonids is not expanded to the extent found in bears. In most procyonids, the process is expressed in the form of a knob-like structure which tends to be grooved.

Based on the shape of the trochlear process as well as other features of the calcaneum, the procyonids can be arranged in three subgroups:

1. *Procyon* (*Iotor* and *cancrivorus*)—*Nasua* (*nasua* and *narica*);
2. *Potos*—*Bassaricyon*; and
3. *Ailurus*—*Bassariscus*.

Both ursids and procyonids have an obvious trochlear process and, in most characteristics,

have similar calcanea. Although the size difference is great between calcanea of members of the two families, the ratios, length of trochlear process divided by width (LTP/W), dorso-ventral height divided by total length ($D-VH/TL$), and least width of body divided by dorso-ventral height ($LWB/D-VH$), are similar (Tables 2 and 4). The larger width in relation to length in ursids does produce a higher W/TL ratio in the bears (Tables 2 and 4). The degree of development of the trochlear process and proximal extension of the trochlear shelf forms the major difference between members of the two families. Other differences are: the bears tend to have broadly joined anterior and medial articular surfaces, the procyonids do not; the bears have a gently curved posterior articular surface which in many of the procyonids is sigmoid; and the greater tuberosity is bulbous in bears and not bulbous in procyonids.

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THE SYSTEMATIC POSITION OF *HELMINTHOGLYPTA TRASKII FIELDI* PILSBRY, 1930 (GASTROPODA: STYLOMMATOPHORA)

BARRY ROTH¹

ABSTRACT: Dissection of the genitalia of the snail described as *Helminthoglypta traskii fieldi* shows that it belongs to the so-called *Helminthoglypta ayresiana* series, a small group of species of coastal, south-central California and the northern Channel Islands. Comparison with other members of the group suggests recognition of it as a distinct species, *H. fieldi*. Pleistocene and post-glacial climatic conditions appear to have influenced distribution of the group.

Helminthoglypta traskii fieldi Pilsbry, 1930, was originally described as a subspecies of *Helminthoglypta traskii* (Newcomb, 1861), a widespread and variable land snail with many named races in southern and Lower California. The latter is the type species of *Charodotes* Pilsbry, 1939, a subgenus principally characterized by the single, thick wall of the penis, in contrast to the double-walled penial structure of *Helminthoglypta, sensu stricto*. While defining the subgenus, Pilsbry (1939) stated that he had dissected only three of its members: *H. traskii*, *H. petricola*, and *H. proles*. He assigned other species and subspecies, including *H. traskii fieldi*, to *Charodotes* provisionally, pending examination of their anatomies.

In September 1972, I collected a series of near-topotypic *H. traskii fieldi* from under sand dune plants just north of the mouth of the Santa Ynez River, Santa Barbara County, California. The dune habitat here is continuous with that at the type locality, Surf, a station on the

Southern Pacific Railroad's Coast Route less than a mile to the south. Adult specimens were dissected and showed genitalial characteristics relating them, not to *Charodotes* and the group of *H. traskii*, but to *Helminthoglypta walkeriana* (Hemphill, 1911), a species of coastal and sub-coastal San Luis Obispo County to the north. Details of shell sculpture and zoogeography support this conclusion. Further data on range and habitat were obtained during field work in October 1972. Recognition of the taxon as a distinct species seems indicated.

Helminthoglypta fieldi Pilsbry Figures 1 and 2

Helminthoglypta traskii fieldi Pilsbry, 1930:66-67, pl. 5, figs. 2-4.

Helminthoglypta traski fieldi Pilsbry, Pilsbry, 1939: 178, fig. 88e.—Webb, 1952:4-5, pl. 2, figs. 3,

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4, 8; pl. 3, figs. 10–14.—Webb, 1954:15, pl. 10, fig. 1.—Smith, 1970:42.

Helminthoglypta walkeriana (Hemphill), Field, 1930:30 (?in part).—Chace, 1951:7 (record from Surf only). [Not *Helix walkeriana* Hemphill, 1911.]

Type material: Lectotype (designated by Baker, 1962: 9), 151516, Academy of Natural Sciences, Philadelphia; paralectotype 327210; three paratypes 152464 in same institution.

Type locality: Surf, Santa Barbara County, California, under ice plants and sage on the beach (Pilsbry).

Original description: "The shell is more elevated than *H. t. phlyctaena*, the height 74 to 77 percent of the diameter (in *phlyctaena* 60 to 66 percent); umbilicus smaller, about 2 mm. wide; post-nuclear whorls are not papillose; last $2\frac{1}{2}$ whorls are spirally engraved with lines cutting the striae, strongly developed on the last whorl. Color cinnamon-brown, with a darker, chestnut-brown band bordered on both sides with chamois. Peristome narrowly expanded, the columellar margin reflected.

"Height 18 mm., diam. 24.5 mm., $6\frac{1}{3}$ whorls.

"Height 20.7 mm., diam. 26.3 mm., $6\frac{1}{2}$ whorls." (Pilsbry, 1930). This description was repeated, with minor changes, by Pilsbry (1939).

ANATOMY

The external anatomy appears to present only the features usual for the genus. The living animal is dark slate grey, the depth of color varying somewhat between individuals. The mantle collar appears lighter, being densely set with whitish mucus glands. The mantle over the lung is tan with sparse black maculation.

Specimens for dissection were prepared by drowning followed by preservation in alcohol. A total of five specimens was dissected.

In gross morphology the dissected reproductive systems agreed substantially with the dissection figured for the species by Webb (1954: pl. 10, fig. 1). The appearance of the lower organs in their everted state was well shown earlier by Webb (1952: pl. 2, figs. 3, 8). Table 1 presents measurements of various organs in the author's dissections. The dart sac, atrium, and base of vagina are enveloped in membranous tissue associated with the mucus glands. The common duct of the mucus glands is extremely thin and fine.

The penial complex is shown in figure 1. The basal section of approximately 4 mm is cavernous, with a single thin wall. This section terminates distally at an opaque, apparently muscular, con-

TABLE 1. Lengths (in mm) of selected reproductive organs of *Helminthoglypta fieldi*

Specimen	1	2	3	4	5
Shell diameter	23	—	21.5	22.5	21
Shell height	18	—	15.5	16	14
Epiphallic caecum	22	28	28	24	23
Epiphallus + penis	26	30	30	28	22
Vagina	1.5	1.5	1.5	3	2
Dart sac + atrium	9	10	10.5	10	8.5
Common mucus duct	2.5	2	2.5	1.5	1.5
Spermathecal diverticulum	57	67	65	58	51
Sp. div. origin from base of spermathecal duct	14	23	12	14	12

striction. Beyond the constriction, the tube is nearly filled by a second, thick-walled inner tube. Longitudinal ridges (four large and five smaller, in the figured specimen) project into the cavity of this inner tube, almost filling it.

The genitalia of *Helminthoglypta traskii*, *H. walkeriana*, and *H. fieldi* are all similar in general character and relative proportions of the organs (cf. Pilsbry, 1939: fig. 63b, *H. walkeriana*; fig. 84b, *H. traskii*). All three share a relatively large dart sac, short common duct of the mucus glands, and long spermathecal diverticulum. These features also appear in *Helminthoglypta ayresiana* (Newcomb, 1861), which Pilsbry (1939) grouped supraspecifically with *H. walkeriana* as the "*Helminthoglypta ayresiana* series."

Helminthoglypta walkeriana and *H. fieldi* have in common a double-walled penis, a pronounced constriction of the penis anteriorly, and a very short vagina. The vagina of *H. fieldi* is proportionally the shortest observed in any *Helminthoglypta* species.

SHELL CHARACTERS

In addition to the author's series of *H. fieldi*, material examined includes specimens in the Geology Department, California Academy of Sciences (including syntypes of *H. walkeriana* and "*Helix* var. *morroensis*" Hemphill, 1911) and the private collections of Allyn G. Smith and S. Stillman Berry.

Helminthoglypta fieldi exhibits the basic sculpture characteristic of both the *H. traskii* group and the *H. ayresiana* series: incised spiral lines which obliquely intersect radial growth striae, the

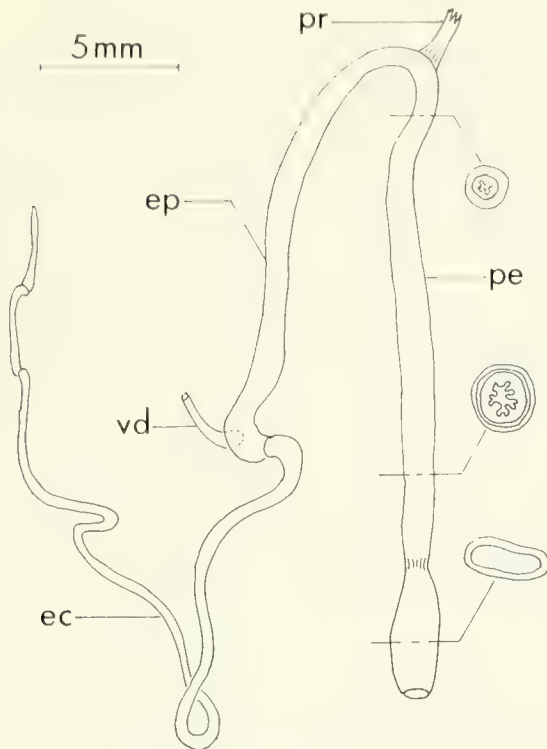


Figure 1. *Helminthoglypta fieldi* Pilsbry, penial complex: ec, epiphallic caecum; ep, epiphallus; pe, penis; pr, penial retractor muscle; vd, vas deferens. Transverse sections slightly enlarged from main drawing.

raised, roughly rhomboidal surfaces thus defined being more or less produced into papillae. In *H. traskii* the degree of papillation is variable from race to race; *H. t. phlyctaena*, for example, the nearest geographic neighbor of *H. fieldi* in the group, is conspicuously papillose on the spire, the papillae being reduced or absent on the last and penultimate whorls. *Helminthoglypta walkeriana* bears moderate to strong papillation, frequently eroded from the early whorls but distributed generally over the body whorl and into the umbilicus. *Helminthoglypta fieldi* tends to develop groups of papillae only immediately behind the outer lip of some adult individuals. Scattered papillae, sometimes in linear groups paralleling growth lines, are rare on other parts of the shell, and many specimens have none at all. Occasional papillae occur in the umbilicus.

The protoconch of *H. fieldi* (described from juveniles hatched to captive topotypic specimens, A. G. Smith collection No. 7954) is minutely granular in texture and more or less evidently

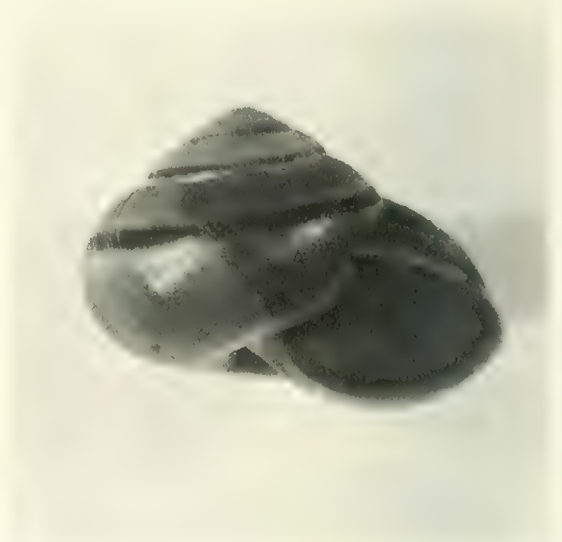


Figure 2. *Helminthoglypta fieldi* Pilsbry, shell. Author's collection #229A; just north of mouth of Santa Ynez River, Santa Barbara County, California.

wrinkled radially, particularly on the dorsal surface. Protoconch and first neanic whorl are covered with short, evenly spaced, stiff periostracal bristles with recurved ends. These are rubbed off all metaneanic and older specimens seen, but a few round, boss-like bristle-bases sometimes remain as far down as the third or fourth whorl. Other authors have sometimes termed these bosses "papillae," but they are periostracal in origin and not homologous to the papillose sculpture previously described for the adult shells. The *H. fieldi* protoconch largely resembles that described by Webb (1941) for *H. dupetithouarsi*, particularly in the presence of recurved bristles. These bristles readily catch on loose organic matter and may help keep the young snails from being blown or washed out of the clumps of vegetable debris in which they usually live—a matter of some gravity in the sand dune habitat.

Apices of well-preserved adults of *H. walkeriana* show substantially the same characters of wrinkling, granulation, and the presence of minute bosses. The apex of *H. walkeriana morroensis* is also similar, with the periostracal bosses more persistent on subsequent whorls.

The shell form of *H. fieldi* is quite constant in all material examined (Fig. 2), with the exception of specimens from one locality, discussed below. Adult specimens (*i.e.*, those with reflected peristome) range in size from 18.4

ECOLOGY AND RANGE



Figure 3. *Helminthoglypta walkeriana* (Hemphill), shell. Syntype, CAS Geology Type Collection 1272; "Near Morro, California."

mm–27.2 mm in diameter and from 14.6 mm–20.9 mm in height. Number of whorls ranges from 5.8–6.3, the mean being just slightly above six. Adult *H. walkeriana* (Fig. 3) show greater variation, ranging from 18.0 mm–28.8 mm in diameter and from 13.6 mm–23.5 mm in height. Whorl-counts of from 5.3–6.2 were noted, the mean being 5.7; more than six whorls were found on specimens approaching or over 27 mm in diameter. Adult *H. walkeriana morroensis* have from 5.2–5.5 whorls. The relationship of whorl number to greatest diameter in these three taxa is shown by figure 4.

The inner lip of *H. fieldi* covers less than half the umbilicus; half or more is commonly covered in *H. walkeriana*. Arcuation of the inner lip, cited as a distinctive character by Pilsbry (1939), is subject to individual variation.

Specimens from sand hills on the north side of Oso Flaco Lake, southwestern San Luis Obispo County (A. G. Smith collection No. 8010 and in the author's private collection), are in some ways intermediate between *H. fieldi* and *H. walkeriana*. They combine the open umbilicus of *H. fieldi*, the large size and tumidity of *H. walkeriana*, and an intermediate degree of papillation. Whorls range from 5.6–6.2, with the mean being 5.8 (Fig. 4). This combination of characters seems confined to this local population, which may represent a past site of interbreeding between the two species.

Helminthoglypta fieldi has previously been reported only from beach habitats in the vicinity of its type locality. There it is associated with the Coastal Strand plant community of Munz and Keck (1965), with sea-fig (*Mesembryanthemum chilense*), Hottentot-fig (*M. edulie*), coastal isocoma (*Haplopappus venetus*), and bush lupine (*Lupinus* spp.) among the conspicuous plants. Dead shells collected by the author a short distance inland from the Santa Ynez River mouth suggest that the snail may range up the river valley, possibly into the agricultural region west of Lompoc. The low hills directly behind the shore are composed of loose, sandy and diatomaceous soils; here occurs more shrubby vegetation, the Coastal Sage Scrub plant community of Munz and Keck (1965), which might provide suitable snail cover as it does for *H. walkeriana* at Morro Bay.

A lot in the California Academy of Sciences (No. 42776) extends the snail's known range some 48 km north to "Pismo" (= Pismo Beach), San Luis Obispo County, also immediately on the coast. Inland, the author has collected it at Halcyon, 5 km southeast of Pismo Beach. A very juvenile specimen from a drainage gully on the northwest slope of Nipomo Mesa, southeast of Oceano, agrees in all details with hatchling *H. fieldi* described above. At Oso Flaco Lake, the snail inhabits the Coastal Strand community.

Helminthoglypta walkeriana appears to be most characteristically a snail of the Coastal Strand and Coastal Sage Scrub plant communities in the vicinity of Morro Bay. It has been found from near sea level at the south end of the bay to 45 m elevation in dunes atop the lowest marine terrace in Montaña de Oro State Park. Inland, as in canyons of the San Luis Range, it is replaced by *Helminthoglypta umbilicata* (Pilsbry, 1898); the latter species also appears more aggressive in colonizing disturbed areas. Field's (1930) record of *H. walkeriana* from "the sandy beaches above Point Conception" certainly refers, at least in part, to the specimens which became the type lot of *H. traskii fieldi* later the same year.

Hemphill's (1911) original locality citations for *H. walkeriana* ("San Luis Obispo") and *H. w. morroensis* ("San Luis Obispo County") were imprecise. The syntypes of the former in the California Academy of Sciences (Geology Type Collection Nos. 1271–1276) are labeled

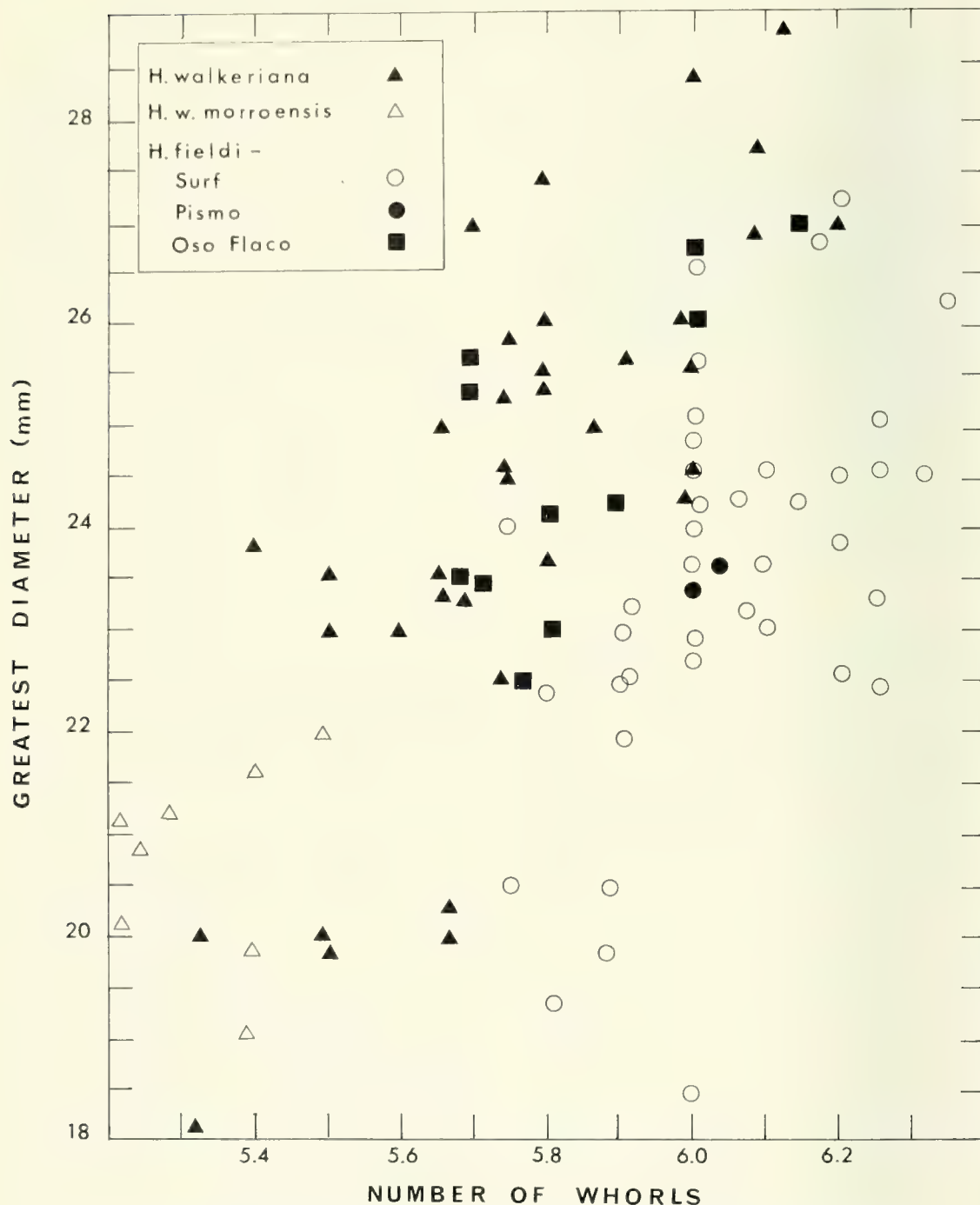


Figure 4. Relationship of whorl number to greatest diameter of shells of *Helminthoglypta fieldi*, *H. walkeriana*, and *H. walkeriana morroensis*. Only adult shells are represented.

"Types" and "Near Morro, California" in Hemphill's handwriting. The syntypes of *H. walkeriana morroensis* (Geology Type Collection Nos. 1260-1270) bear the Hemphill label "Types" and

"Near San Luis Obispo City." Later collecting has confirmed the occurrence of the snails at these respective locations; they, and not the published citations, should be considered the

type localities. A lot (A. G. Smith collection No. 8510) from three miles (4.8 km) south of Cayucos, San Luis Obispo County, appears to be identical with *H. w. morroensis* from the city of San Luis Obispo. Further field work is necessary to establish fully the geographic limits of all three taxa.

Factors influencing local distribution may include moisture, in the form of a drip zone under plants which condense the coastal fogs, and the presence of stabilized sand around the roots of dune plants. Cooper (1967) has discussed the postglacial development and present characteristics of sand dunes in the areas under discussion.

Helminthoglypta fieldi was cited as rare and of limited range by Smith (1970). At present it is very numerous and easily collected at the Santa Ynez River mouth; but development of the dune area for recreational or other purposes could conceivably eliminate the colony. *Helminthoglypta walkeriana* has at least theoretical protection in Montaña de Oro State Park and the sandspit area of Morro Bay State Park, which is well-advisedly closed to vehicular traffic.

DISCUSSION

The anatomical and conchological characters discussed above indicate that the snail in question belongs to the *Helminthoglypta ayresiana* series of Pilsbry (1939) of coastal, south-central California and the northern Channel Islands (San Miguel, Santa Rosa, Santa Cruz, and Anacapa). This view was anticipated by Chace's (1951) recording "*H. walkeriana*" from Surf, where only *H. fieldi* occurs. That paper, an abstract, does not contain a discussion or explanation of the implied synonymy. It is this author's opinion that the pattern of differences between the snails examined, combined with the distributional data, favors recognition of *H. fieldi* as a distinct species. The former interpretation—considering *H. fieldi* a subspecies of *H. traskii*—requires viewing the snail as an aberrantly northward-ranging member of a group predominantly associated with the Los Angeles Basin and the Peninsular Ranges physiographic province of southern California.

The range of *H. fieldi* consists of a series of more or less disjunct, local populations, possibly relicts of a broader, former distribution. No zone of present sympatry between *H. walkeriana*

and *H. fieldi* has yet been found. The aberrant population at Oso Flaco Lake may be the result of past contact and interbreeding between the two species. Not enough material has been seen to clarify the phyletic relationship of *H. walkeriana* to *H. w. morroensis*; but the diagnostic features of the latter, strong papillation and absence of spiral lines, are variably expressed among shells from a single locality.

The following key to members of the *H. ayresiana* series, based on shell characters, illustrates some of their structural relationships.

- 1a. Papillation present over all or most of body whorl 2
- b. Papillation absent or confined to a few papillae in umbilicus or behind outer lip of adult shells 3
- 2a. Incised spiral lines strong, not overridden by papillation *H. walkeriana*
- b. Spiral lines absent or weak, overridden by papillation *H. walkeriana morroensis*
- 3a. Shell surface shiny, vitreous; body whorl enlarging rapidly (Mainland) *H. fieldi*
- b. Shell surface dull, earthy; body whorl closely coiled throughout (Channel Islands)
H. ayresiana (+ subsp. *sanctaecrucis* Pilsbry, 1927)

Among the taxa of the *H. ayresiana* series, number of whorls increases from north to south. The southernmost member, *H. ayresiana* has from 6.25–7 whorls.

It seems plausible that the ancestors of *H. ayresiana* reached their present island location overland like the mammoth and other Pleistocene biota at a time when a peninsular connection existed between the islands and the mainland. Mid- or late Pleistocene paleogeography would have permitted such migration (Weaver, 1969; Weaver and Doerner, 1967); the presence of fossil snails well down in late Quaternary subaerial deposits on San Miguel Island (Johnson, 1971) favors the earlier date. Since the land connection existed along the axis of the Santa Monica Mountains (cf. Valentine and Lipps, 1967: fig. 4), at about the latitude of southern Ventura County, the ancestral *H. ayresiana* series must then have occupied territory south of its present distribution on the mainland. This may have coincided with a southward displacement of climatic zones accompanying a glacial-pluvial stage, the present distribution of the series having come about later as a result of xerothermic conditions following the Wisconsin glaciation.

A similar process has been invoked by Axelrod (1967) to explain the presence on the islands of relict plant species having their closest relatives to the north.

The capacity of land snails for passive dispersal, as by rafting, however, should not be underestimated. Aestivating *Helminthoglypta*, sealed to solid materials, may be excellent marine travelers, and the northern Channel Islands are not very far offshore. Santa Rosa Island, the most distant, is only 44 km from the mainland. Land snails evidently reached the southern Channel Islands over water (Valentine and Lipps, 1967). Species which inhabit the immediate coast may be especially susceptible to such transport. This model too, however, is enhanced by the concept of ancestral *H. ayresiana* series members south of the group's present mainland range, along the Santa Barbara Channel-Embayment coast.

A subject for further study is the relationship of Pilsbry's subgenus *Charodotes* to other members of *Helminthoglypta* such as the *H. ayresiana* series. As noted above, except for the doubly tubed penis, the genitalia of the *H. ayresiana* series bear a strong resemblance to those of *H. traskii*. A study conducted by Berry (1953) indicated that the distinction between single-walled and double-walled penis may not always be so clear-cut, at least in certain groups within the genus.

Another snail which deserves consideration in the same context is *Helminthoglypta traskii phlyctaena* (Bartsch, 1916), for which a genitalial description apparently has not been published. It inhabits Santa Barbara and Ventura Counties. Berry (1953: 338) treated it as a full species and intimated affinities with *H. ayresiana* and *H. walkeriana*, but he did not elaborate on this theme. Pilsbry (1939) compared it to *H. fieldi*, but the author has seen no intergradation between the two to support the racial relationship expressed in Pilsbry's statement, "*H. t. fieldi* is the coastal form, *phlyctaena* the inland, Coast Range race." The California Academy of Sciences collection contains one lot of *H. t. phlyctaena* (No. 24842) from Jalama Creek, Santa Barbara County, near the coast. Curiously, the genitalia figured by Pilsbry (1939: fig. 84b) for *H. traskii* are cited from "near Las Cruces, Santa Barbara County," which should be *H. t. phlyctaena* territory.

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A NEW GENUS AND SPECIES OF GECKO (SAURIA: GEKKONIDAE) FROM IRAN AND IRAQ

JAMES R. DIXON¹ AND STEVEN C. ANDERSON²

ABSTRACT: A thorough examination of the osteology of eastern hemisphere species of gekkonid lizards formerly placed in the genus *Phyllodactylus* indicates that these species either belong to generic taxa presently in the synonymy of *Phyllodactylus* or represent new genera. *Phyllodactylus elisae*, an isolated member of the eastern hemisphere "*Phyllodactylus*" found only in western Iran and eastern Iraq, represents one of the new genera. It differs from western hemisphere *Phyllodactylus* and the Old World forms by the absence of cloacal sacs and bones, loss of one phalanx in the fourth finger and toe, loss of the second epibranchial arch of the hyoid, and possession of a cartilaginous rod-shaped hypoischium.

A new species is described from the northern Iraq-Iran border area, differing from *P. elisae* in size of body and tail tubercles and granules, absence of tubercles on upper arm and rear of head, larger snout-vent length, color, and color pattern.

For the past 15 years, one of us (Dixon) has been involved in a study of the eastern hemisphere species of the gekkonid genus *Phyllodactylus*. A thorough examination of the osteology of the eastern hemisphere species indicates that they are not *Phyllodactylus* (*sensu stricto*), but are either new genera or represent generic taxa presently in the synonymy of *Phyllodactylus*.

Dixon and Kluge (1964) described a new

genus (*Crenadactylus*) for the Australian species *Phyllodactylus ocellatus*, and Dixon and Kroll (in press) have recently resurrected the genus *Paroedura* Gunther, for nine species of *Phyllo-*

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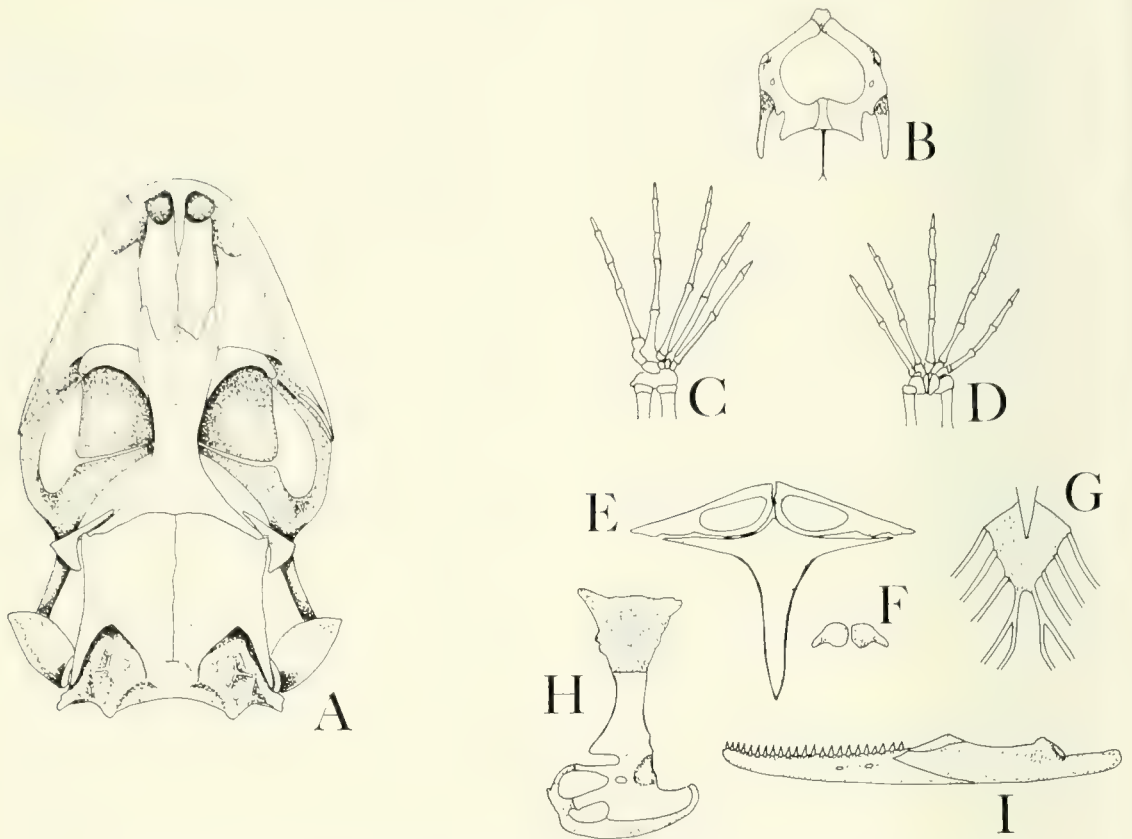


Figure 1. Some aspects of the osteology of the gekkonid lizard genus *Asaccus (elisae)*. (A) dorsal view of skull; (B) ventral view of pelvic girdle; (C) dorsal view of pes; (D) dorsal view of manus; (E) ventral view of clavicles and interclavicle; (F) dorsal view of paired atlas; (G) ventral view of sternum and sternal ribs; (H) lateral view of the scapulo-coracoid element; (I) lateral view of the left dentary.

dactylus from Madagascar. Manuscripts dealing with the remaining Australian, African, and Asian species of *Phyllodactylus* are in progress.

Phyllodactylus elisae, as currently recognized, was described by Werner (1895) from the ruin of Nineveh, near Mosul, Iraq. Nikolsky (1907) described *P. eugeniae* from Dezful, Iran, apparently not being aware of Werner's 1895 description of *elisae*. Werner (1917) pointed out the similarities between the two species and placed *eugeniae* in the synonymy of *elisae*. This action was verified by Wettstein (1951) and Wermuth (1965).

The external squamation of *P. elisae* is much like that of species from the western hemisphere and consists of enlarged tubercles arranged in longitudinal rows on the dorsum and tail, scattered randomly on the head and limbs, and one large pair of terminal, leaf-like lamellae on the

fingers and toes. However, the internal anatomy of *P. elisae* differs in several important features from species of the western and eastern hemisphere. One of these differences (absence of cloacal sacs and bones) was pointed out by Kluge (1967). We believe the magnitude of osteological and anatomical differences that separates *P. elisae* from other gekkonid genera warrants the erection of a new generic taxon. With reference to the absence of cloacal sacs, we propose the following name.

Asaccus, new genus

Type species: *Phyllodactylus elisae* Werner 1895.

Diagnosis: *Asaccus* differs from all other gekkonid genera in the following combination of characters: cloacal sacs and bones absent; second epibranchial arch of hyoid present; phalangeal formulae for manus and pes, 2-3-4-4-3; stapes perforate



Figure 2. *Asaccus griseonotus*, new species: (1) Palagawrah Cave, Sulaimaniyah Liwa, Iraq, c. 925 m. (type locality?); (2) 38.5 mi from Shahabad (direction not recorded), Kermanshah Province, Iran (type locality). *Asaccus elisae*: (3) Balad Sinjar, Mosul Liwa, Iraq, c. 770 m; (4) Nineveh, Mosul Liwa, Iraq (type locality); (5) Jarmo, Kirkuk Liwa, Iraq, c. 800 m; (6) Baghdad, Iraq; (7) Dezful, Khuzestan Province, Iran, c. 160 m (type locality for *Phyllodactylus eugeniae* Nikolsky); (8) Abu Karaniyeh, Khuzestan Province, Iran (type locality for *P. eugeniae*); (9) between Masjed Soleyman and Batvand, Khuzestan Province, Iran, c. 300 m; (10) Sar-i-Gach, Khuzestan Province, Iran, c. 450 m; (11) Pol-e Abgineh, Fars Province, Iran, c. 950 m.

(stapedial foramen present); 28 amphicoelous, sacral and presacral vertebrae; atlas paired; parietals paired; nasals paired, with long projection of premaxillary between nasals; anterior tip of mesoscapula lacking osseous or cartilaginous connection with precoracoid process; interclavicle shield-like; 3 pairs of sternal ribs, 2 pairs of mesosternal ribs; one large fenestra in clavicle; supratemporal absent; angular absent; frontal single; 9–10 premaxillary teeth, 56–60 total dentary teeth and 48–52 total maxillary teeth; 14 scleral ossicles in each eye; hypischium cartilaginous, rod-like (Fig. 1).

Distribution: *Asaccus* is known from eastern Iraq, east of the Euphrates River, and western Iran, west of the Zagros Mountains (Fig. 2). Arnolds (1972) described a new species from the southeastern tip of the Arabian Peninsula which he designated *Phyllodactylus gallagheri*. Although we have not examined specimens of this new taxa, we suspect that it is yet another representative of the genus *Asaccus* and

would therefore extend the range of the genus southward onto the Arabian Peninsula.

Asaccus elisae (Werner)

Phyllodactylus elisae Werner 1895. Verh. Zool.-bot. Ges. Wien, 45:14.

Type locality: Ruin of Nineveh, Iraq.

Phyllodactylus eugeniae Nikolsky 1907. Ann. Mus. Zool. St. Petersburg, p. 268. Type locality: Dezful and Abu-Garia, Iran.

Diagnosis: A moderately small gecko (maximum snout-vent length 57 mm avg. 50.2 mm), tubercles of dorsum, limbs, and tail large, length of individual tubercle more than 64 percent ($M = 67.5$ percent) of ear diameter; 8–14 longitudinal rows of enlarged dorsal tubercles; 10–12 large tubercles across rear of head between ears; 2–12 enlarged tubercles on upper arm, above elbow; tail tubercles arranged in whorls, each whorl separated by 3–4 rows of granules (Fig. 3).

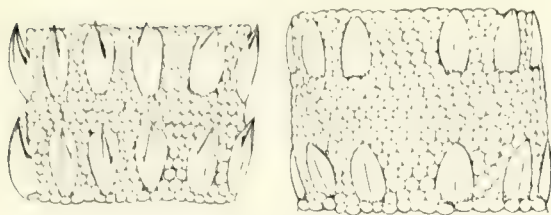


Figure 3. Dorsal view of the proximal whorls of tubercles about the tail. Note that the large tubercles on the right (*A. griseonotus*) are flattened and not strongly keeled, while those on the left (*A. elisae*) are elevated and strongly keeled. The dorsal body scales and tubercles are similar to those illustrated here.

each tubercle of dorsum separated from other such tubercles by 2–3 granules. Ground color usually dark brown with none to five dark brown, dorsal body bands; each tubercle usually tipped with white, giving freckled appearance to color pattern; tail with five brown to black bands and five white bands, each of equal width, venter whitish.

Remarks: In addition to *A. elisae*, a series of nine specimens, which represent a new species of *Asaccus*, were taken from Palegawra Cave, Iraq, and 38.5 mi from Shahabad, Iran (Fig. 2). Superficially, these individuals resemble *elisae* in most meristic characters. Without a detailed comparison of individuals of both populations, it would be extremely difficult for a person unfamiliar with gekkonid squamation to distinguish the two forms. A detailed analysis of the salient features of the new taxon reveals that some of the characters differ significantly from those of *elisae* at two and occasionally three, standard errors. However, the known range of variation of each of these characters matches or strongly overlaps that of *elisae*. In addition to the meristic data, however, there are other profound differences and, therefore, we consider the new taxon distinct from *elisae* and propose the following name.

***Asaccus griseonotus*, new species**

Holotype: Field Museum of Natural History (FMNH) 170824; adult ♀, collected by Dan Womochel and Anthony F. De Blase, 29 August 1968, 38.5 mi from Shahabad, Kermanshah, Kerman Prov., Iran. **Paratypes:** FMNH 170817–23, topoparatypes; FMNH 74553, Palegawra Cave, Sulaimaniyah Liwe, Iraq.

Distribution: Known only from the type locality and Palegawra Cave, Iraq.

Diagnosis: A large member of the genus with a maximum snout-vent length of 71 mm (avg. 61.8 mm), lacking enlarged tubercles across the rear of head and on dorsal surface of upper arm; tubercles of dorsum and limbs small, length of individual tubercle less than 46 percent ($M = 39.4$ percent) of ear diameter; 6–7 rows of granules separate enlarged tubercular tail whorls (Fig. 3); each tubercle of dorsum separated from its adjacent tubercle by 4 to 5 granules; dorsal color ash gray with 20 to 30 small, dark gray spots scattered over dorsum.

Description of holotype: Rostral slightly more than twice as wide as high, its dorsal edge shaped in a broad “W”; two internasals, somewhat hexagonal, with rounded edges, their median edges in broad contact bordered posteriorly by three granules and postnasal of each side; nostril surrounded by rostral, labial, internasal and two postnasals; first labial in broad contact with lower edge of nostril; shallow depression between internasals, moderate depression in frontal region; 10 scales between eye and nostril; scales in posterior loreal region about five to six times larger than interorbital scales; 17 scales across snout at level of third labial; 18 scales across anterior edge of orbits; 20 interorbital scales; eye large, its diameter contained in snout length 1.9 times; eyelid with three rows of granules and one larger outer row, of which the last five to seven scales are pointed; diameter of ear contained in eye diameter 1.9 times; ear opening large, scales of anterior and posterior border granular, subequal; rear of head granular with a few larger, almost subequal scales intermixed; 9/9 supralabials and 7/7 infralabials to point below center of eye; mental bell-shaped, about as long as wide, bordered posteriorly by two postmentals; postmentals twice as long as wide, their median edges in broad contact, followed by second pair of subpostmentals that are followed by an undulating transverse row of 16 granules, followed by 20 granules in second row; postmentals contact first and second labials of each side.

Dorsum with 11 longitudinal rows of enlarged keeled tubercles that are somewhat flat and whose length is less than half the diameter of ear; paravertebral row of enlarged dorsal tubercles with 31 tubercles from nape to base of tail, 16 between axilla and groin; paravertebral rows separated from each other by three to four rows of granules; six rows of tubercles reach nape, and six to base of tail; each tubercle of enlarged dorsal series separated from each other by three to five granules; postanal tubercles small, indistinct; venter with 37 longitudinal and 95 transverse rows of scales.

Dorsal surface of upper arm with flattened, imbricate scales (enlarged tubercles absent); forearm with 9 to 12 enlarged tubercles interspersed among smaller scales; dorsal surface of thigh with 8 to 12 and lower leg with 10 to 20 tubercles scattered among smaller scales; lamellae formula for hand

TABLE 1. Comparison of meristic features of *A. elisae* (n = 38) and *A. griseonotus* (n = 9). Those marked with an asterisk are considered significant.

	<i>A. elisae</i> Mean (range) $\pm$ SD (SE)	<i>A. griseonotus</i> Mean (range) $\pm$ SD (SE)
* Ventral scales longitudinal	33.6 (28-43) $\pm$ 2.8 (0.49)	38.4 (35-41) $\pm$ 2.0 (0.67)
* Ventral scales transverse	88.0 (82-100) $\pm$ 5.8 (1.1)	96.6 (94-101) $\pm$ 2.6 (0.9)
Dorsal tubercles longitudinal rows	11.6 (8-14) $\pm$ 1.3 (0.2)	10.8 (10-13) $\pm$ 0.9 (0.3)
* Paravertebral tubercles from head to tail	27.3 (22-31) $\pm$ 1.8 (0.3)	30.0 (24-33) $\pm$ 2.4 (0.8)
Paravertebral tubercles between axilla-groin	15.5 (12-20) $\pm$ 1.8 (0.3)	17.2 (15-19) $\pm$ 1.3 (0.4)
Granules bordering postmentals	16.2 (13-20) $\pm$ 1.9 (0.4)	15.6 (12-17) $\pm$ 1.5 (0.5)
Fourth toe lamellae regardless of size	13.1 (11-16) $\pm$ 1.3 (0.2)	14.7 (13-16) $\pm$ 0.8 (0.3)
Scales between nostril and eye	12.9 (11-16) $\pm$ 1.4 (0.2)	11.0 (10-12) $\pm$ 1.0 (0.3)
Scales across snout at level of third labial	16.6 (14-19) $\pm$ 1.2 (0.2)	16.8 (15-18) $\pm$ 1.0 (0.3)
Scales across midorbital region	19.3 (16-23) $\pm$ 1.9 (0.3)	20.9 (19-23) $\pm$ 1.3 (0.5)

10-10-11-12-11, foot 8-11-13-13-13; claw clearly visible when viewed from below; terminal lamellae composed of two large leaf-like structures, slightly more than three times longer than wide.

Measurements (in mm): snout-vent length 62.0, axilla-groin length 29.6, leg length 32.7, arm length 26.6, tail length 66.0, head length 18.2, head width 11.3, snout length 7.5, eye diameter 4.0, ear diameter 2.2.

Color in alcohol: Ground color ash gray, dorsum with 25 small, dark gray spots scattered evenly over body from nape to base of tail; limbs with faint gray smudges on dorsal surfaces, ventral surfaces of limbs and body uniform dirty white; tail with seven gray to black bands, gray bands proximal, black distal, with white interspaces of equal width; tip of tail tan.

Variation: Little variation was noted in color or color pattern. All specimens have enlarged, transverse rows of scales beneath the tail and all have a laterally compressed tail tip. For variation of meristic characters see discussion on comparisons and associated table.

Comparisons: Basically, *A. griseonotus* is a large gecko with small tubercles and *A. elisae* is small with large tubercles. However, this is somewhat deceptive because *elisae* has small granules surrounding the large tubercles whereas *griseonotus* has large granules surrounding small tubercles. This quantitatively results in an almost

identical number of enlarged tubercles when they are counted in a standard manner. Table 1 compares the meristic data for the two species.

Natural History: Nothing is known regarding the natural history of the new form, other than the fact that Reed collected specimens in the cool, humid environment of limestone crevices of Palegawra Cave in northeastern Iraq (Reed and Marx, 1959: 97-98). Such an environment would be similar to that of the culvert in which Anderson collected *A. elisae* in Khuzestan, Iran (Anderson, 1963: 442). The Street Expedition to Iran in 1962 collected specimens of *A. elisae* in caves in Fars Province. In Baghdad, *A. elisae* is a house gecko, according to Weber (1960: 153). Known food items for *A. elisae* include spiders, ants, beetles, mosquitos, and moths. All of the females of *A. elisae* examined contained ovarian eggs, the largest 2 mm in diameter; all were collected in June, July, August, and late December.

Specimens Examined: *Asaccus elisae* (38). IRAN: 5 km SE Pol-e Abgineh, Fars Province. California Acad. Sci. (CAS) 102520-22, FMNH 141307-09, 141311; Pol-e Abgineh, FMNH 141306; Kuretu, British Mus. Nat. Hist. (BMNH) 1921.3.30.1-3; between Masjed Soleyman and Batvand, CAS 86436-43, 86525-29, 86352, 86339-40; Sar-i-Gach, CAS 86432. IRAQ: Baghdad, FMNH 19695; Arbil, BMNH 1961.1501-03; Jarmo, FMNH 74551; Mosul, FMNH

19696, 19702-03; no specific locality, Museum Comparative Zoology, Harvard Univ., 25905.

Asaccus griseonotus (9). IRAN: 38.5 mi from Shahabad, FMNH 170817-24. IRAQ: Palegawrah Cave, Sulaimaniyah, Liwe, FMNH 74553.

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RESEARCH NOTES

FEEDING IN THE PORCELAIN CRAB, *PETROLISTHES CINCTIPES* (RANDALL) (ANOMURA: PORCELLANIDAE)

Petrolisthes cinctipes (Randall, 1839), the porcelain crab, is a common anomuran of the higher to mid-intertidal zones of both cobble beaches and mussel beds along the northern California coast. It has been noted to fan plankton and detritus from the water (MacGinitie and MacGinitie, Natural history of marine animals, p. 305, 1968); and, in captivity, to feed on suspensions of either finely-chopped *Fucus* sp. or *Cladophora* sp. (Kurup, Biol. Bull., 127:97-107, 1964).

Petrolisthes erimerus, a close relative of *P. cinctipes*, is known to eat pelagic diatoms, benthic diatoms, and green algal filaments. The movement of its mouth parts and the structure of its gut suggest that it is a filter feeder (Knudsen, Pacific Sci., 18:3-33, 1964).

Mechanics of feeding in the Porcellanidae were described for *Porcellana longicornis* (Nichol, J. Mar. Biol. Ass. U. K., 18:87-107, 1932). By alternately flexing the endopodites of its third maxillipeds, this animal trapped floating particles. These food particles were removed from the filtering setae on the third maxillipeds by the setose ends of the endopodites of the second maxillipeds. The inner mouthparts appeared to select and sort food.

This paper attempts to describe the feeding process in *Petrolisthes cinctipes* from the capture of food to its absorption in the midgut. Foods both as accepted by animals in the laboratory and found in the stomachs of field specimens are listed. Means by which the anomuran rejects particles unsuitable for digestion are discussed.

METHODS

Seventy-four living *Petrolisthes cinctipes* were collected during 1971 and 1972 at five locations in northern California (along the south side of Little Head, Trinidad, 15 crabs; about one mile north of Trinidad, 28 crabs; at Pigeon Point, San Mateo County, 17 crabs; at Pebble Beach, Crescent City, seven crabs; and by the Heeser Drive Public Fishing Access, Mendocino, seven crabs). The animals were kept in aquaria of running, filtered sea water at the Marine Laboratory, Trinidad, during 1971-72, and at the Department of Biological Science, College of San Mateo, San Mateo, during late 1972.

To observe the feeding process, respiratory currents, and general behavior, two to five animals were selected from those in the aquaria. These porcelain crabs were placed in a plastic pan containing sea water and some rocks. After the animals took

cover, food materials were introduced by pipetting or by dipping a dish of food into the water. The animals were offered a variety of foods. Currents were followed by dropping the dye eosin either between the first antennae or above the carapace. Actions of the appendages, rates of movement of the appendages, foods accepted, directions of the currents, and other feeding behavior were recorded during 0.5 to 2.0 hour observation periods. Each animal was watched at least once. A total of 45 observations of feeding activity were made over a period of two years.

Twenty-eight *P. cinctipes* were preserved (either in 70 percent isopropanol or in 10 percent formalin in sea water) for dissection. Dissections were made under 30 $\times$ magnification, while smears of stomach contents and fecal material were examined at 100 $\times$ magnification.

RESULTS AND DISCUSSION

The length of a feeding period in *Petrolisthes cinctipes* varied with the food supply. Specimens in a nearly-sterile aquarium continued feeding for hours, while those in a medium full of food sometimes stopped within 0.5 hours after starting.

The second maxilla did not seem to function as part of the feeding appendages. Its location lateral to the mouth field and at the origin of the outgoing respiratory current suggests that it helps produce the respiratory current. However, since this appendage lies under the exoskeleton, its activities cannot readily be seen.

Only once out of forty-five times, *Petrolisthes cinctipes* was seen to obtain food by means other than suspension feeding. On this one occasion, one animal seized with its chelae a piece of tissue from the mantle of a dead *Mytilus californianus*. The tissue was shredded before being passed to the endopodites of the third maxillipeds. These endopodites pushed the tissue to the endopodites of the second maxillipeds, which in turn held it in front of the mandibles. The mandibles chopped the tissue into smaller pieces, which were ingested.

Six times, porcelain crabs captured long filaments of algae. These filaments either were caught by the endopodites of the third maxillipeds, or became entangled on the second antennae. The filaments were transferred from the place of capture to the endopodites of the second maxillipeds. The algae then were held in front of the mandibles, which cut them into pieces which were ingested. However, usually the crabs rejected algal filaments by using the chelae to pick the filaments out of the mouth parts. The filaments then were tossed away from the animals.

The usual mode of feeding, suspension feeding

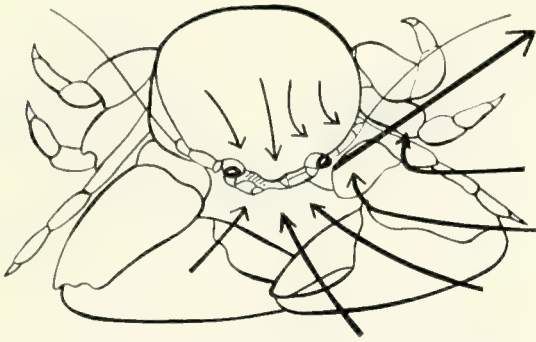


Figure 1. Feeding currents and outgoing respiratory current of *Petrolisthes cinctipes*.

on small material, begins with a stroking motion of the endopodites of the third maxillipeds. The endopodites straighten dorsally, one at a time. Fine, tapered, pinnate setae spread out from the last three segments, forming a net. (Henceforth, this filtering net and its segments will be called the fan.) The fan is held open and then bent downward toward the basis of the appendage. As one fan bends downward, the other straightens upward. The entire process usually takes less than a second, with an average rate of 80 strokes per minute. If food is scarce, the fans may be held extended for up to ten seconds at a time. The segments of the fan can swivel, allowing both fans to stroke in the same direction. In this case, the endopodite closest to the source of food straightens, swivels to face the oncoming food, opens the fan, turns back to the original position, and then bends downward. Currents generated by the stroking of the endopodites can pull in nauplii of *Artemia salina* from a distance of 4 mm from the dactyls of the fans. These currents bring in material ventrally, dorsally and laterally, except where either the respiratory current dominates over them or the action of the maxillipeds interferes with them (Fig. 1).

Contrary to the observations of MacGinitie and MacGinitie (1968), the second maxilliped does not fan plankton and detritus from the water. Instead, the setose end of the endopodite reaches up to the fan of the third maxilliped when the fan bends downward. This end sweeps gathered material toward the mouth.

Incoming particles appear to be sorted by both the first maxillipeds and the first maxillae. The first maxillipeds move rapidly during feeding, but since they are covered by the second maxillipeds, it has been impossible to diagnose their activities. Particles to be ingested pass between the first maxillae. The mandibles remain slightly agape during most of the feeding period (closing only about three or four times per minute) as long as the animal is capturing fine particles.

Certain particles (notably the eggs of *Artemia*

salina) are sorted for rejection before ingestion. These particles move dorsally along the setae of the first maxillae, instead of passing between them. They are transferred to the terminal portion (the "flagellum" of Nicol, 1932) of the exopodite of either the second or third maxilliped on the side from which the respiratory current is originating. While one flagellum continues to beat with the respiratory current, the other with the particles flicks them into the current, which carries the rejected material away. If too many rejected particles build up, the crab snaps its abdomen, sending upward a blast of water that clears the filtering appendages.

Ingested material passes into the short esophagus, which leads into the large, chitinous stomach. Food seems to be sorted by circular bands of setae, each band of a given size, located in the cardiac stomach. After sorting, the food is ground into a relatively homogeneous chyme by the gastric mill. Digestible material goes through the pyloric stomach to the white, branched digestive glands lateral to the pyloric stomach. Undigestible particles (particularly fine sand grains) traverse the long hindgut to be ejected as long, stringy, mucus-covered feces.

The minimum size of food taken by *Petrolisthes cinctipes* is governed by the spacing between the branch hairs on the setae of the fans. Depending on the size of the animal, these hairs are spaced from 3 to 30 microns apart. Hairs on the distal portion of the setae average 21 microns apart, while the spacing of the proximal hairs tapers to an average 9 microns apart.

Foods most acceptable to the captive specimens were the diatoms *Skeletonema costatum*, and *Thalassiosira* sp., unidentified ciliated protozoans, and newly-hatched nauplii of *Artemia salina*. Five animals took filaments of *Spirogyra* sp. Only one accepted tissue from *Mytilus californianus*. The crabs would not eat suspensions of goldfish food, dead cyclopoid copepods, muscle tissue from *Cancer* sp., *Plocamium* sp., *Polysiphonia* sp., or pieces of finely-chopped fish. Eggs of *Artemia salina* usually were rejected into the respiratory current.

Stomachs of freshly-killed field specimens varied in their contents. In all but two of the nineteen examined, fine sand grains were found. The next most common contents were bits of plant detritus (in eight stomachs), the diatom *Coscinodiscus* sp. (five stomachs), and two taxa of foraminiferans (five stomachs). In one stomach each were the diatom *Isthmia* sp., the diatom *Chaetoceros* sp., pieces of filamentous red algae, a harpacticoid copepod, a hydroid polyp, and a cypris larva.

Kurup (1964) called *Petrolisthes cinctipes* a scavenger as well as an algal feeder. The scarcity of times that it was observed to feed on dead animal tissue, the frequent rejection of algal filaments and of chopped fish or invertebrate muscle tissue, and the varied stomach contents, however,

suggest that most of its food is obtained by suspension feeding rather than by either scavenging or selectively feeding on algae.

Like *Petrolisthes eriomerus*, *Petrolisthes cinctipes* eats many diatoms. The latter seems to eat more foraminiferans and less green algal filaments than the former. The food preferences seem to resemble most closely those of the British anomuran *Porcellana longicornis*, found by Nicol (1932) to feed primarily on detritus and microorganisms, and occasionally on both mussels and algae. Both *Petrolisthes cinctipes* and *Porcellana longicornis* fan the water with the endopodites of the third maxillipeds, and use the setose ends of the endopodites of the second maxillipeds to remove gathered material. However, the swiveling action of the third maxillipeds, in which the endopodites of both sides faced in the same direction, was not observed in *Porcellana longicornis*.

I thank John DeMartini, Jack Yarnall, and Gary Brusca of the California State University of Humboldt, and Howard Monroe of the College of San Mateo for their helpful suggestions and for reviewing the manuscript.

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Accepted for publication June 29, 1973.

THE LONGNOSE PUFFER, *Sphoeroides lobatus* (STEINDACHNER) ADDED TO THE MARINE FAUNA OF CALIFORNIA

On 23 December 1972, an unknown fisherman on Redondo Pier caught a longnose puffer, *Sphoeroides lobatus*, on a hook baited with a live anchovy. He presented the fish alive to personnel of Redondo Sportfishing, a commercial concession on the pier, and they in turn gave it to Jerry Goldsmith, Marineland of the Pacific. Two weeks later it was still alive in an aquarium at Marineland of the Pacific, but because of the scarcity of *Sphoeroides* in Californian waters, it was deemed more valuable as a preserved specimen than as potential food for one of the larger predators in Marineland's fish tank where it would have to be housed.

Although a puffer which was caught in the vicinity of San Pedro on 15 May 1941 and presented to the Cabrillo Beach Marine Museum appears to be *S. lobatus* (because of its elongate snout), the Redondo Beach fish is the first positive record for the species from Californian waters. The 1941 specimen was not properly identified before it was cast as a wall mount, and in the process of making the cast, features

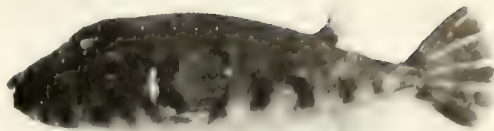


Figure 1. Longnose puffer, *Sphoeroides lobatus*, 232 mm SL (275 mm TL) caught on hook and line from Redondo Pier, 23 December 1972.

which distinguish *S. lobatus* from *S. annulatus* were destroyed.

The Redondo Beach specimen (Fig. 1) was 232 mm SL (275 mm TL) and weighed 450 g. No information is available regarding maximum size for the species, nor on various aspects of its life history. With this capture, however, its range as now understood is from Redondo Beach to Panama and at the Galapagos Islands.

Because descriptive material for distinguishing *S. lobatus* from *S. annulatus* is both confusing and inadequate, and to preclude misidentification of future specimens, the following simple key is offered:

A dark fleshy flap present above each pectoral fin near midback; bony interorbital narrow and deeply concave; interorbital width projects into snout length more than 4 times *S. lobatus*

No fleshy flaps above pectoral fin on back; bony interorbital wider, slightly concave to convex; interorbital width projects into snout length less than 3.5 times *S. annulatus*

Sphoeroides annulatus, the bullseye puffer, apparently has been taken only twice in Californian waters (1857 and sometime prior to 1880), and only at San Diego. Thus, occurrences of either species are noteworthy and should be reported.

I wish to thank Lillian Dempster, California Academy of Sciences, San Francisco, who helped me with several references which were not available locally; Jerry Goldsmith who recognized the fact that puffers were unusual in local waters and graciously donated this specimen in the interest of science; and Jack W. Schott, California Department of Fish and Game, Long Beach, for taking the picture used as Figure 1. The puffer is now preserved in the fish collection of the Natural History Museum of Los Angeles County (LACM 33366-1).

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Accepted for publication September 26, 1973.

THE SECOND RECORD OF THE GIANT
SEADEVIL, *CERATIAS HOLBOLLI*,
FROM CALIFORNIA, WITH
NOTES ON ITS LIFE
HISTORY

Based upon some badly mangled remains found in the stomach of a sperm whale, *Physeter catodon*, which had been harpooned during November 1970 about 115 km west of San Francisco, Rice (Bull. So. California Acad. Sci., 91:158, 1972) reported the first occurrence of the giant seadevil, *Ceratias holbolli*, from Californian waters. Fourteen months after the first specimen was found a second individual (Fig. 1) was captured in an otter trawl which was being fished on the bottom in 293 to 375 m from lat. 41°23.8'N long. 124°29.9'W to lat. 41°22.2'N long. 124°30.3'W (near Redding Rock off the mouth of Redwood Creek, Humboldt Co., California). Emery Wilson, skipper of the trawler *Mineo Bros.*, informed me that during the tow which yielded the giant seadevil, the net dropped into the head of a submarine canyon and undoubtedly fished deeper than the 200 fms. (375 m) registered by his fathometer.

This seadevil, a female 525 mm SL (700 mm TL) and weighing 4990 g, was netted on 11 January 1972. It had a parasitic male 37 mm SL attached to the midline of the belly at a point approximately one head length in advance of the anal fin. Although the illicium was missing on the female, it did not appear to have been broken off during capture or subsequent handling. The loss of its illicium could have affected its feeding behavior in that it no longer could lure prey species within easy "striking" distance, and thus would be forced to seek out food items not normally utilized. Unfortunately, I was unable to find any accounts of stomach contents for *Ceratias holbolli*, so I could not compare the items found in the specimen at hand with those reported

for "normal" individuals. The stomach of the Redding Rock seadevil contained one slightly digested short-spine thornyhead, *Sebastolobus alascanus*, 117 mm SL; the head end including beaks of an unidentified squid; a 25 mm long basal fragment from the arm of a starfish, *Petalaster foliolata*; and a parasitic tapeworm. The squid beaks were compared with those from *Loligo opalescens*, *Rossia pacifica*, and *Moroteuthis robusta*, three of the most abundantly taken squid in that area, but they did not match any of these.

In an effort to obtain additional life-history data, I removed the otoliths from the female as well as the parasitic male, and examined them for indications of age. Those from the female had six excellent hyaline growth zones, whereas no annuli could be distinguished on the microscopic sagittae from the male. The smallest female with a male attached appears to be a 460 mm SL specimen reported by Abe (Proc. Japan Acad., 43:797-800, 1967) from the coast of Japan; the male was only 32 mm TL, which also appears to be a record for smallness. Since the Japanese specimen probably represents minimum size at maturity, and since the six hyaline zones on the otoliths of the Redding Rock seadevil very likely are true annuli, it is reasonable to assume that the female *Ceratias holbolli* does not reach maturity until an age of five years, at least.

I wish to thank the skipper of the trawler *Mineo Bros.*, Emery Wilson, for saving the giant seadevil and turning it over to Lawrence F. Quirollo, California Department of Fish and Game, Eureka, who took special pains to see that it was properly preserved. Jack W. Schott, California Department of Fish and Game, Long Beach, took the photograph which appears as Figure 1. The Redding Rock seadevil has been deposited in the fish collection of the Natural History Museum of Los Angeles County (LACM 33718-1).

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Accepted for publication September 26, 1973.

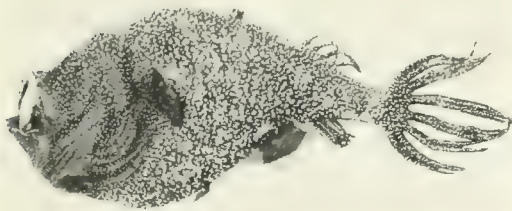


Figure 1. Female *Ceratias holbolli*, 525 mm SL, with attached parasitic male, 37 mm SL, trawled near Redding Rock, California, on 11 January 1972. The large gelatinous mass with a dark center which appears immediately in front of the anal fin is extruded ovarian tissue.

CHROMOSOMES AND THE STATUS OF
RHAMPHOLEON MARSHALLI
BOULENGER (SAURIA:
CHAMAELEONIDAE)

Recently, Broadley (Arnoldia, 5:1-6, 1971) recommended that the chameleon species *marshalli* be transferred from the genus *Chamaeleo* to *Rhampholeon*. The bases for this recommendation were the similarities in hemipenial, cranial and external mor-

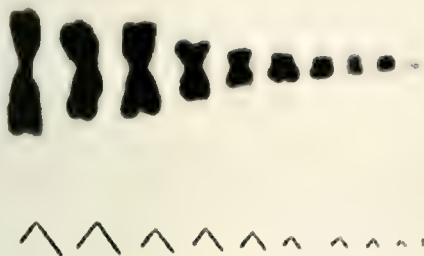


Figure 1. Photomicrograph of haploid complement of mitotic metaphase chromosomes of *Rhampholeon marshalli* (LACM 76768, female), above (longest chromosome = 7.5 micra); and an idiogrammatic representation of a haploid complement of chromosomes of *R. spectrum* (drawn from Matthey and Van Brink, 1960), below.

phological characteristics between *R. marshalli* and *R. platyceps* Gunther. We present here an analysis of the chromosomes of *R. marshalli* which also suggests that the affinities of *marshalli* lie with *Rhampholeon* rather than *Chamaeleo*.

Matthey and Van Brink (Bull. Soc. vaudoise Sci. Nat., 67:333-348, 1960) presented chromosomal data for 27 of the 69 species of chameleons recognized by Hillenius (Beaufortia, 8:1-92, 1959). Among the species analyzed was *R. spectrum*, the type species of *Rhampholeon*. The diploid chromosome numbers for the entire group ranged from 36 (12 macrochromosomes and 24 microchromosomes) down to 20 (18 macrochromosomes and 2 microchromosomes). *Rhampholeon spectrum* was unique within the group in having 20 chromosomes. Species with the most similar chromosome numbers and morphologies to *R. spectrum* (22 to 24 chromosomes with no to 4 microchromosomes) are restricted in distribution to Madagascar.

We analyzed chromosomes prepared by a colchicine-hypotonic citrate technique (see Lowe, Wright, and Cole, Mamm. Chromos. Newsletter, 22:201-203, 1966) from bone marrow, spleen, intestine and/or testes of four specimens of *R. marshalli* (LACM 76767-70, 1 male, 3 females) from Bunga Forest, Vumba Mountain, Rhodesia. Based on our analysis, the chromosomes of *R. marshalli* (Figs. 1 and 2) are similar to those reported for *R. spectrum* by Matthey and Van Brink (1960). The karyotype consists of the following: nine pairs of biarmed chromosomes (metacentric and submetacentric) with no distinct break or division into size classes and one pair of acrocentric chromosomes, the smallest of the series, for a total of 20 chromosomes and 38 chromosome arms, with no distinguishable sex chromosomes. The

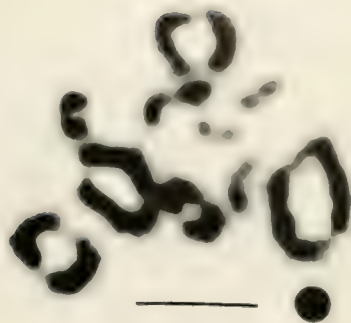


Figure 2. Photomicrograph of diakinesis chromosomes of *Rhampholeon spectrum* (LACM 76767, male) illustrating 10 bivalent figures (line represents 10 micra).

only apparent differences between the karyotypes of *R. marshalli* and *R. spectrum* lie in chromosome pairs 2 and 3 (from left to right in Fig. 1). These two pairs in *R. marshalli* are more even in size and slightly more metacentric than those of *R. spectrum*.

The overall similarity of the karyotypes of *R. marshalli* and *R. spectrum* and the apparent uniqueness of this condition (both number and morphology) in chameleons is interpreted as additional evidence of the affinities of *marshalli* with *Rhampholeon*.

JOHN W. WRIGHT, *Section of Herpetology, Natural History Museum of Los Angeles County, Los Angeles, California 90007*, and DONALD G. BROADLEY, *Keeper of Herpetology, National Museums and Monuments of Rhodesia (Umtali Museum), Umtali, Rhodesia*.

Accepted for publication October 1, 1973.

TWO ADDITIONAL RECORDS OF *TADARIDA MACROTIS* AND *EUDERMA* *MACULATUM* FROM SAN DIEGO, CALIFORNIA

One adult male of *Tadarida macrotis* was captured on 7 October 1970 in the bathroom of a second story apartment in Mission Beach, San Diego, California. The bat apparently entered through an open window during the night and was found the following morning crawling down the bathtub drain. The specimen was taken to the University of San Diego where it was identified as *T. macrotis*. External measurements of this individual were

(mm): total length 124; tail length 52; hind foot 9; ear (notch) 23; and forearm 61. This is the third report of the Big Free-tailed Bat in San Diego and the fourth occurrence in California (Shamul, Proc. U. S. Nat. Mus., 78:19, 1931; Huey, J. Mamm., 13:160, 1932; and Huey, J. Mamm., 35:435, 1954).

Howell (J. Mamm., 1:112, 1920) proposed that *T. macrotis* needs high points from which to begin flight. Both of Huey's records were from comparable high locations and the capture of our specimen on the second story may support Howell's contention. The bat is now a specimen (No. 60, alcoholic) in the Natural History Museum of the University of San Diego.

In September 1955 a adult female of the Spotted Bat, *Eudermia maculatum* was found hanging from a second story window sill by Bernice Farrens at the University of San Diego. The specimen was collected, identified and preserved (alcoholic), and set aside. It was not until recently that the bat was measured and positively identified. The external measurements of this bat were (mm): total length 102; tail length 43; hind foot 11; tragus 14; ear (notch) 39; and forearm 52. Although this rare bat has been reported throughout California, none, to our knowledge, have been reported in San Diego County. This bat is now a specimen in the Natural History Museum of the University of San Diego (No. 61).

Special thanks are due Bernice Farrens for kindly lending us the specimen of the Spotted Bat.

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Accepted for publication March 9, 1973.

A NEW GENUS AND SPECIES OF HAPLOPORID TREMATODE (HAPLO- PORIDAE: TREMATODA) FROM AUSTRALIAN MULLET

While in the Parasitology Department at the University of Queensland, Brisbane, Australia (1970-71), I found some haploporid trematodes possessing an undivided cecum in the intestines of mullet collected in the Brisbane River. A new subfamily with two new genera was established for them (Martin, Proc. Helm. Soc. Washington, 40:112-117, 1973). This paper adds another genus and species to that subfamily.

The worms were fixed without pressure in hot 5 percent formalin, cleared in methyl benzoate and mounted in Canada Balsam. Measurements are expressed in microns unless otherwise indicated. Averages are in parentheses.

Paraunisaccoides, new genus

Diagnosis: Body fusiform, tegument spined, oral sucker subterminal, acetabulum in anterior half of body. Prepharynx elongate, pharynx well developed at or slightly posterior to acetabular level, esophagus shorter than prepharynx, cecum elongate, partially divided posteriorly. Vitellaria elongate cords in posterior half of body. Testis in hind body, ovary immediately anterior. Laurer's canal and seminal receptacle uterinum present. Uterus between ovary and hermaphroditic duct. Eggs relatively large and few. External seminal vesicle saccular. Internal seminal vesicle, prostate cells, prostate bulb, a portion of uterus, hermaphroditic duct with denticulate pads, and muscular ring enclosed in hermaphroditic sac. Genital pore immediately anterior to acetabulum, transversely elongate.

Type species: *P. lobolectithus*, new species.

Paraunisaccoides lobolectithus, new species

Figures 1 and 2

Specific diagnosis: Description based on two ovigerous specimens with the characters of the genus. Body spines more numerous anteriorly, both suckers ringed with spines. Body length 1.85, 2.07 mm; body width 266, 406. Eyespot remnants present. Oral sucker 96, 112 long and 100, 112 wide. Acetabulum 93, 143 long and 78, 156 wide. Prepharynx 426, 684 long. Pharynx 109, 112 long and 131, 137 wide. Esophagus 112, 249 long, cecum 390, 518 long, composed of large cells. Unicellular glands along esophagus and prepharynx, the latter's ducts passing to lip of oral sucker. Genital pore midventral anterior to acetabulum, crescent shaped in one specimen. Hermaphroditic sac 258, 286 long and 96, 118 wide. Hermaphroditic duct lined with pads bearing tiny denticles. Internal and external seminal vesicles filled with sperm. Testis near posterior end of body, 239, 345 long and 168, 202 wide. Ovary oval 109, 140 long and 100, 109 wide. Eggs with thin yellow shells, partially collapsed so that measurements are near approximations, 71-93 (86) long and 56-59 (58) wide. Excretory bladder Y-shaped with arms reaching ovarian level.

Holotype: No. 7114, deposited in the Hancock Parasitology Collection, University of Southern California.

Host: *Mugil cephalus* L., sea mullet.

Site: Intestine.

Type locality: Brisbane River, Brisbane, Queensland, Australia.

Paraunisaccoides differs from *Unisaccoides* mainly in the nature of the vitellaria, ribbon-like in the former and follicular in the latter. *Paraunisaccoides* also has a longer prepharynx, pads of hermaphroditic duct with denticles instead of spines, a more restricted uterus and a shorter excretory bladder.

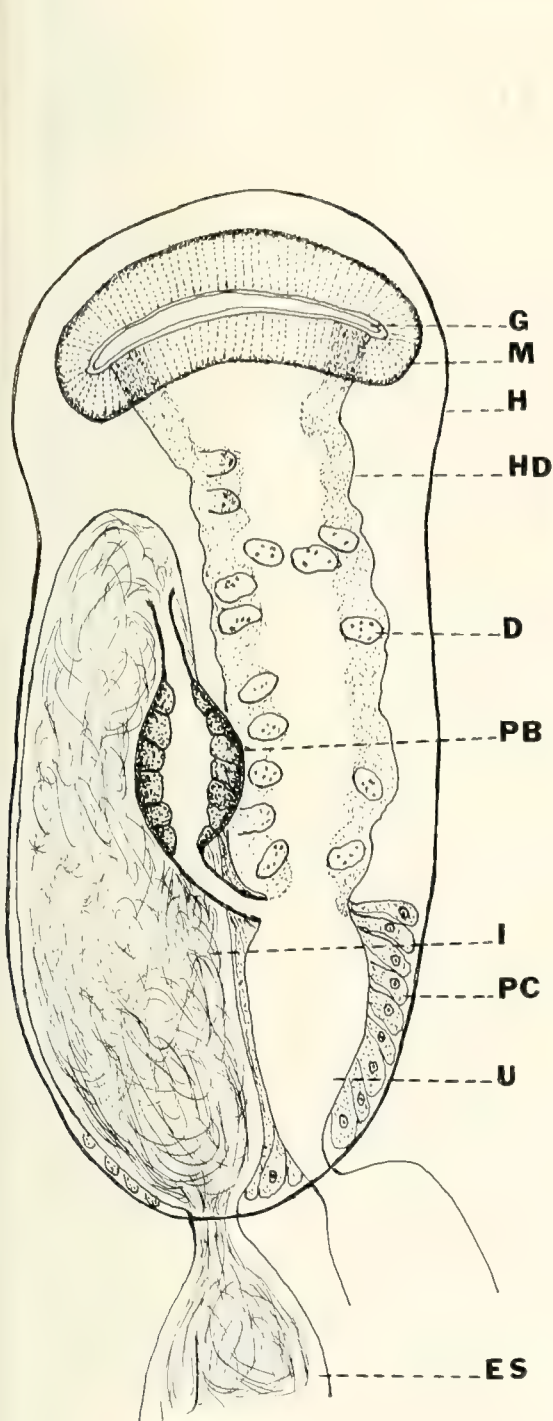


Figure 1. Terminal genitalia of *Paraunisaccoides lobolecithus*, new species. D, denticulate pad; ES, external seminal vesicle; G, genital pore; H, hermaphroditic sac; HD, hermaphroditic duct; I, internal seminal vesicle; M, muscular ring; PB, prostatic bulb; PC, prostate cells; U, uterus.

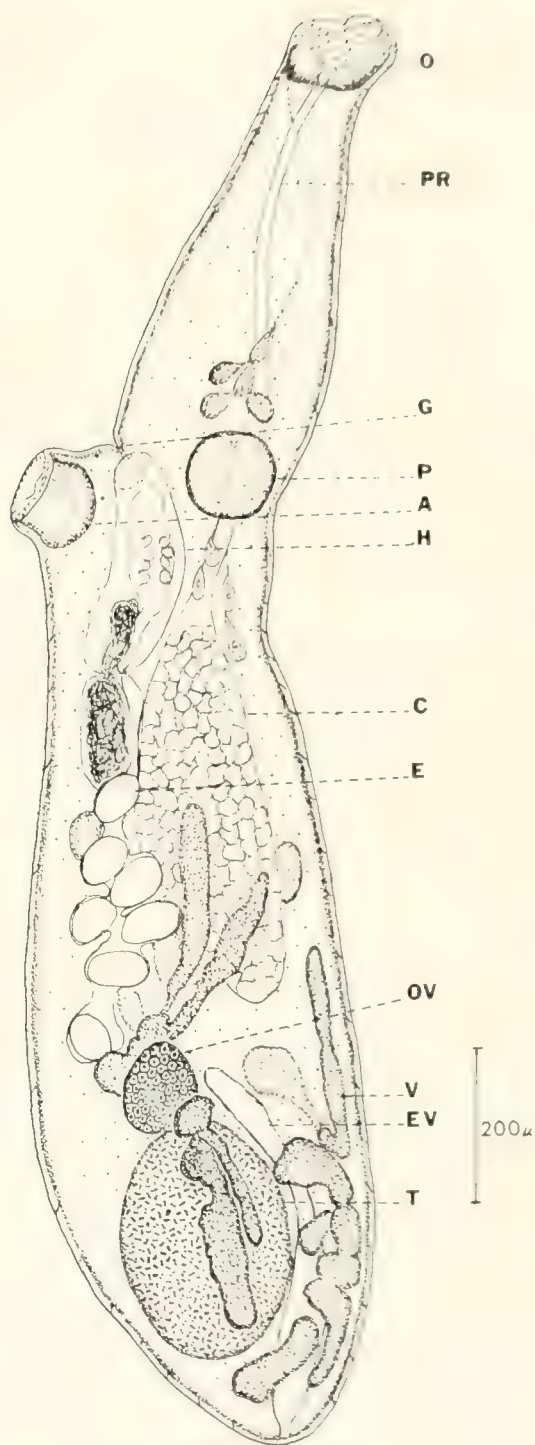


Figure 2. Lateral view of *Paraunisaccoides lobolecithus*, new species. A, acetabulum; C, cecum; E, egg; EV, excretory vesicle; G, genital pore; H, hermaphroditic sac; O, oral sucker; OV, ovary; P, pharynx; PR, prepharynx; T, testis; V, vitellaria.

The subfamily Unisaccinae is emended to include species with elongate vitellaria.

I am greatly indebted to J. F. A. Spreti, Head of the Parasitology Department, University of Queensland, for the use of laboratory facilities and encouragement in many ways; to John Pearson, Reader in Parasitology for assistance; to Jim Davie for help in

collecting fish; and to the National Science Foundation for support (NSF 66962).

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EDITORIAL: CRITICAL REVIEW OF MANUSCRIPTS

As indicated in the Instructions for Authors (inside back cover), all manuscripts submitted to SCAS BULLETIN are reviewed by referees who critically read for scientific content, originality, and clarity of presentation, and who assist the editors in making judgments as to acceptability for publication. The reviewers also assist authors by offering constructive suggestions which may lead to improvement of the text or illustrations of manuscripts. By contribution of their time and professional expertise the referees measurably enhance the quality of SCAS BULLETIN.

In behalf of our readers, authors, and ourselves we thank the following reviewers for valuable editorial assistance in recent months: Phillip A. Adams, Louis F. Baptista, James A. Blake, Thomas E. Bowman, Bayard H. Brattstrom, James M. Brennan, Joseph A. Chapman, Fenner A. Chase, Murray D. Dailey,

James R. Dixon, George F. Fisler, Anthony J. Gaudin, Hugh H. Genoways, Janet Haig, William Hand, John William Hardy, Joseph E. Haring, Richard B. Loomis, John S. McAnally, Patsy A. McLaughlin, Walter B. Miller, William S. Morris, Peter A. Morrison, Martin L. Morton, Michael Neushul, I. M. Newell, Donald R. Patten, Anthony J. Provenzano, Jr., Donald J. Reish, Jay M. Savage, Elbert Sleeper, Andrew Starret, John S. Stephens, Arnold H. Studemund, Robert Stockhouse, Dale Straughan, Lowell P. Thomas, Stuart L. Warter, Joel Weintraub, Harrington Wells, Dieter H. Wilken, Adrian M. Wenner.

PATRICK H. WELLS, Technical Editor

JAMES DALE SMITH, Managing Editor

ANNOUNCEMENT: 1974 ANNUAL MEETINGS

The 1974 annual meetings of the Southern California Academy of Sciences will be held on May 3 and 4, 1974 at California State University, Fullerton. Technical papers are solicited from the fields of natural and social sciences.

Abstracts of no more than 150 words must be typed on 3 × 5 cards and *must be received no later than March 22, 1974*. The first line of the abstract is to include author(s), student or professional, preferred section (see below), and type of projection equipment, if needed. **Send abstracts to:** David L. Walkington, *Dept. Biological Science, California State University, Fullerton, California 92634*.

Technical sessions—Anthropology, Archaeology, Botany, Earth Science, Entomology, Experimental Biology, Folklore, History, Invertebrate Zoology, Marine Science, Vertebrate Zoology, Psychology, Economics, and Geography (other

sections will be opened to accommodate demand). Special interest symposia will be presented.

Student awards will be presented in the Natural Science and Social Science Divisions. First award in each division will be \$150.00; second award in each division \$75.00.

A.A.S. Grant in Aid of Research—\$150.00 will be awarded to a high school, undergraduate, or graduate student submitting the most outstanding research proposal in the sciences. *Application forms available from Takashi Hoshizaki, Dept. Biological Science, California State University, Fullerton, California 92634*.

Banquet—The annual banquet will be held the evening of May 4; presentation of awards will be made at this time. *Speaker:* Stanley M. Greenfield, Assistant Administrator, Environmental Protection Agency; *Topic:* General problems of environmental protection: evolution and enforcement.

INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and November) and includes articles in English in any field of science. Non-members will be assessed a page charge of \$40.00 per page. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current *AIBS Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, achieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous reference of pronouns, and logically placed modifiers.

MANUSCRIPT PREPARATION

It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit *at least one additional copy with the original*, on 8½ × 11 opaque, non-erasable paper, double spacing the entire manuscript. *Do not break words at right-hand margin anywhere in the manuscript.* Footnotes should be avoided. Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper must accompany a *feature article*.

A **feature article** comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, methods, results, discussion and conclusions, acknowledgments, and literature cited. Avoid using more than two levels of subheadings.

A **research note** is usually one to six typewritten pages and rarely utilize subheadings. Consult a recent issue of the BULLETIN for the format of *notes*. Abstracts are not used for notes.

Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. Omit periods after standard abbreviations: 1.2 mm, 2 mi, 30 cm, but Figs. 1-2. Use numerals *before* units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International Code of Botanical Nomenclature (Lawjouw *et al.*, 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan *et al.*, 1958), and the International Code of Zoological Nomenclature (Stoll *et al.*, 1961). Special attention should be given to the description of new taxa, designation of holotype, etc.

The **literature cited** section should include six or more references; entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452-458.

Brattstrom, B. H. 1969. The condor in California. Pp. 369-382 in Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

If fewer than six references are cited they should be inserted in text as follows:

(McWilliams, Insect mimicry, p. 216, 1970); (Holmes and Speak, J. Mamm., 54: 452-458, 1971); (Brattstrom, The Condor in California, Pp. 369-382, in Vertebrates of California, 1969).

Tables and figures (line drawings, graphs, or black and white photographs) **should not repeat data contained in the text.** The author must provide *numbers* and *short legends* for tables and figures and place reference to each of them in the text. Legends should be typed on a separate sheet of paper and placed at the end of the manuscript. **Illustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size;** ordinarily they should be no more than twice the size of intended reduction and should not exceed 8½ by 11 inches in size. Photographs *must* be printed on glossy paper. Submit one photoduplicated copy of each illustration. All illustrations accompanying **Research Notes** will be reduced to one column width.

A **cover illustration** will be printed on the cover of each issue. This may be an illustration pertaining to an article in the issue or one of general scientific interest. Such illustrations along with a brief caption should be sent to the technical editor for review.

PROCEDURE

All manuscripts should be submitted to the Technical Editor, Patrick H. Wells, Department of Biology, Occidental College, Los Angeles, California 90041. **Evaluation of a paper** submitted to the BULLETIN begins with a critical reading by the technical editor; several referees also check the paper for scientific content, originality, and clarity of presentation. Judgments as to the acceptability of the paper and suggestions for enhancing it are sent to the author at which time he may be requested to rework portions of the paper considering these recommendations. The paper is then re-submitted and may be re-evaluated before final acceptance after which it is sent to the managing editor.

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COVER: Aerial view of a 150' high Arctic Pingo (Eskimo for "conical one") just south of Tuktoyaktuk, Mackenzie River Delta, Northwest Territories, Canada. Pingos are produced by the arching of an impervious surface sheet of permafrost which is forced up by water which is under pressure. The natives hollow out Pingos and use them for freezer storage.

Photo by Donald B. Bright, Dept. of Biological Science, California State University, Fullerton.

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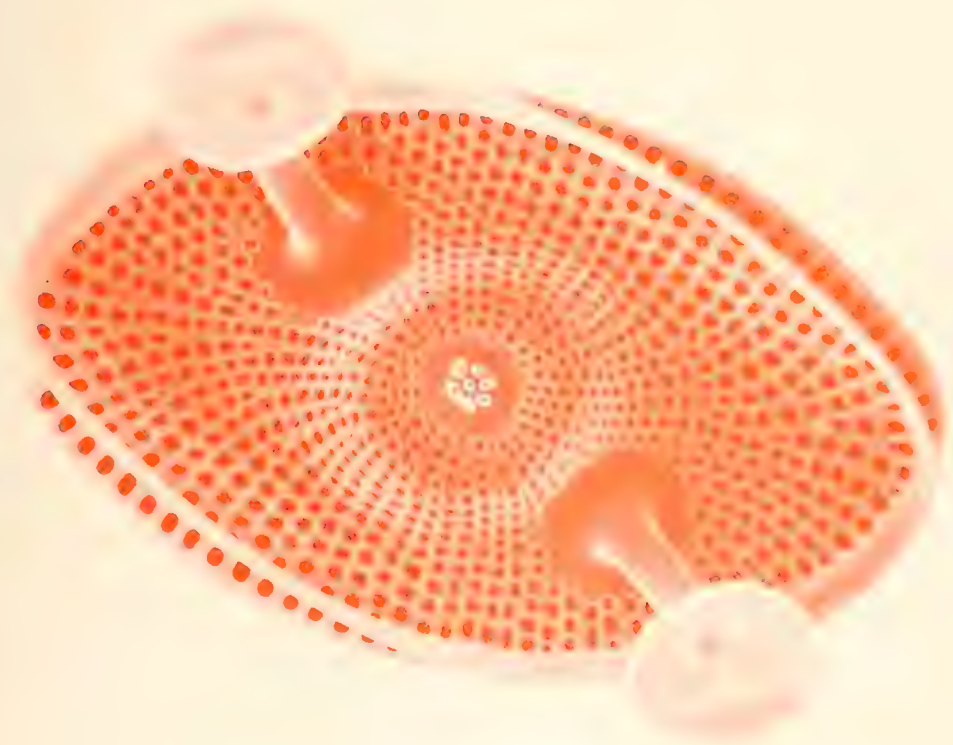
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NUMBER 1

A NEW SPECIES OF POLYCHAETOUS ANNELID (ARABELLIDAE) PARASITIC
IN *DIOPATRA ORNATA* (ONUPHIDAE) FROM SOUTHERN CALIFORNIA

RAYMOND R. EMERSON¹

ABSTRACT: A new species of polychaetous annelid of the family Arabellidae is described. Various sizes were found parasitic in the coelomic cavity of a single specimen of the onuphid polychaete *Diopatra ornata* collected near Port Hueneme. Movement of the parasite may occur through the septal walls of the host but not laterally through the dorsal or ventral mesenteries.

Polychaetes are known to occur primarily as free living or sedentary forms and occasionally as commensals but, rarely are they found as parasites. Parasitism by arabellid polychaetes, which in some cases may represent only a transitory stage in their development, occurs principally in other polychaetes. A review of the literature by Pettibone (1957) lists ten species of parasitic arabellids of which nine species are parasitic in members of the polychaete families Eunicidae, Onuphidae, Terebellidae, Syllidae, and Spionidae; the remaining species occurs in the echiuroid family of Echiuroidea. Five species, or half of those reported, are parasitic in eunicids and onuphids. Both host families are closely related to the arabellids and all three are members of the superfamily Eunicea. The instances of parasitism by arabellid polychaetes within other onuphid polychaetes as reported by Pettibone includes the following records: *Drilonereis bendicti* (Pettibone) within *Onuphis magna* (Webster), numerous specimens of *Notocirrus spiniferus* (Moore) from a single specimen of *Diopatra cuprea* (Bosc), (Allen, 1952), and a single specimen of *Drilonereis caulleryi* (Pettibone) in an anterior fragment of *Onuphis* (*Nothria*) *conchylega* (Sars). In addition Hartman (1968) found *Arabella iricolor* (Montagu) in specimens of *Diopatra ornata* (Moore).

In 25 specimens of the tube worm *Diopatra ornata* collected near Port Hueneme, California in May 1972, one was found to contain several

size classes of a new species of endoparasitic arabellid, which is described herein. This is contribution No. 10 of the Santa Catalina Marine Biological Laboratory.

RESULTS

One specimen of *Diopatra ornata* was observed to contain a segmented worm moving under its body wall. An incision was made along the dorsolateral margin of several parapodia located midway along the body which allowed removal, with forceps, of a small polychaete. The host specimen, a female, consisted of 195 segments complete with pygidium and was 10 mm wide and 150 mm long. Four parasites were eventually removed from the host and some were fixed while in the host for subsequent sectioning. The largest specimen was 60 mm long, 1.0 mm wide with 241 segments. The body was heavily pigmented and the head had a functional jaw apparatus and two pairs of eyespots. The smallest specimen was 20 mm long and 0.5 mm wide and lacked eyespots, jaw apparatus, and pigmentation. The largest specimen exited from the 33rd segment of the host without assistance. The host displayed no excitation or unusual behavior during this event. The escape from the host may have occurred via one of the nephridiopores which are well-de-

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veloped anteriorly, as no apparent tissue damage was observed.

Freed parasites and segments of the host containing additional parasites were fixed in 10 percent formalin and Dubosq Brasil. The latter were embedded in Paraplast, cut at 8μ , and stained in Erlich's hematoxylin and eosin, using the method of Humason (1967). The parasite was not in the gut cavity but, appears to be confined to the coelomic cavities of the host (Fig. 1A). Movement of the parasite had occurred through the septal walls of the host but not laterally through the dorsal or ventral mesenteries (Fig. 1B).

The host female contained significantly fewer oocytes in the coelom than did *Diopatra* females unafflicted with the parasite. The gametic products may represent the major food source for the later growth stages of the parasite which are complete with a functional jaw apparatus and digestive tract. Consumption of the reproductive products would also provide additional space within the coelomic cavity of the host for the parasitic stages. Smaller or juvenile parasites, which lack jaws may be unable to actively consume the thick shelled oocytes, but could be supported by consumption of the coelomic fluid or absorption of dissolved nutrients from it.

The well-developed eyes and body pigmentation of the largest specimen indicate an active free living stage in the life cycle of the parasite. The time spent within the coelomic cavity and the means of entering the host organism are unknown.

The true incidence of infection in the population of *Diopatra ornata* located near Port Hueneme cannot be predicted from the small sample of 25 specimens of which only one was found to be infected. However, it is of interest that several hundred specimens of *Diopatra ornata* from a population located near Catalina Island have been examined and none of the specimens were infected.

Arabella endonata, new species

Description: The holotype is complete and has 241 segments. It is 60 mm long and 1.0 mm wide with-

out parapodia. A brownish pigmentation covers the ventral and dorsal portion of the body, but the parapodia are unpigmented. Smaller specimens completely lack pigmentation. The ovate prostomium is slightly longer than wide, with a pair of faint longitudinal grooves ventrally. Two pairs of dorsal eyespots are present in a transverse row. The outer pair is slightly larger and appears to be subepidermal (Fig. 2A).

The first two segments are apodus. Parapodia are similar in all setigers. The presetal lobes are rounded while the well-developed postsetal lobes are digitiform and directed slightly dorsally. The notopodium consists of two dorsolateral papillae supported by a single stout notopodial aciculum. The neuropodium is also supported by a single aciculum (Fig. 2B).

Setae are bilimbate, doubly curved, and with a fine tip. The wings are smooth or finely denticulate along the border. The main shaft is striated (Fig. 2C). Three to four setae are present in a parapodium.

The mandibles are triangular and fused (Fig. 2D). The paired maxillary carriers are separate along their entire length except near the posterior end where they appear to be joined; each carrier has a spatulate anterior end. The presence of an unpaired carrier was not noted. All of the maxillary plates are distally falcate. The maxillary formula of the type specimen is $10+10 - 6+5 - 4+4 - 1+1$. The left maxilla I has a more pronounced falcate or hooked condition (Fig. 2E) than the apposing maxillary tooth.

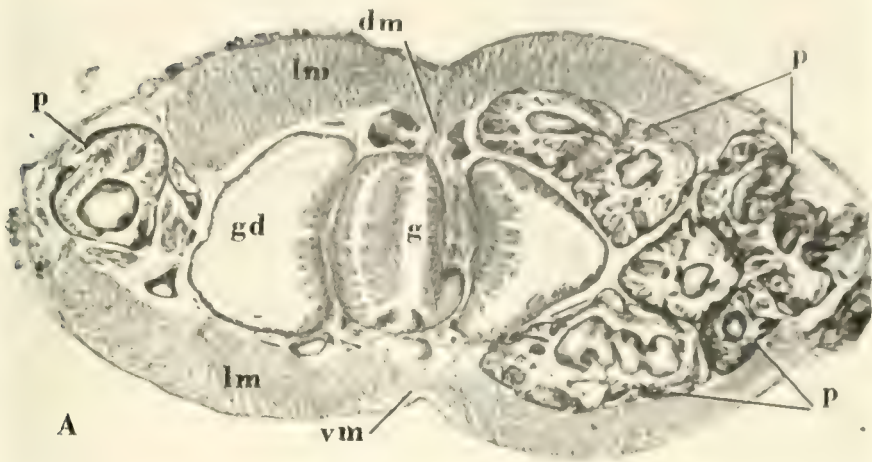
The holotype and paratypes have been placed in the collection of the Allan Hancock Foundation, University of Southern California, Los Angeles, California.

Distribution: The host organism containing the type specimen was collected from sandy silt substrate at a depth of 50-60 feet off the southern California coast near Port Hueneme.

Etymology: The name *Arabella endonata* (*endo*, from the Greek *end* = within, and *nata*, a contraction of the specific name of the host *Diopatra ornata*) is appropriate as the species is endoparasitic within *Diopatra ornata*.

Remarks: Aside from the parasitic nature of *Arabella endonata* it is easily separated from other free living species of *Arabella* previously identified from California and Western Mexico (Fauchald, 1970; Hartman, 1944). *Arabella endonata* is distinguished from *Arabella geniculata* (Claparede), *A. iridescens* (Treadwell), *A. mimetica*

Figure 1. A. Cross section through segment 100 of *Diopatra ornata* showing parasites within the coelomic cavities of the host. Dorsal mesentery (dm), ventral mesentery (vm), parasite (p), gut (g), gut diverticulum (gd), longitudinal muscle (lm), and dorsal blood vessel (dv). B. Longitudinal section of several genital segments of *Diopatra ornata* showing parasite penetration through a septal wall of the host (arrows). Septum (s), parasite (p), parasite jaw apparatus (pj), gut (g), and longitudinal muscle (lm).



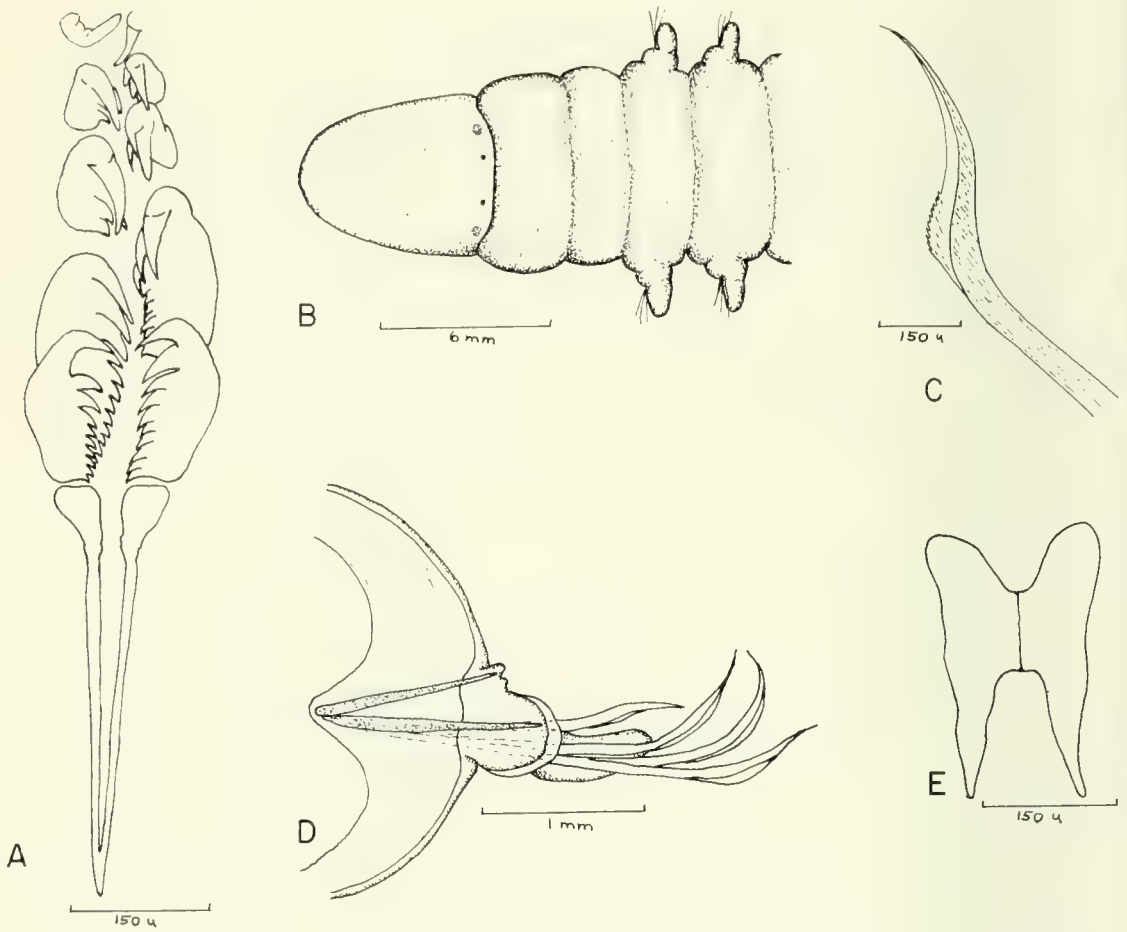


Figure 2. *Arbella endonata*, new species. A, maxillary plates and carriers; B, anterior end in dorsal view; C, bilimbate seta; D, setiger 100 in anterior view; E, mandibles.

(Chamberlin), and *A. novecrinita asymmetrica* (Crossland), by its possession of eye spots. *Arabella semimaculata* (Moore) and *A. iricolor* (Montagu) with 2–3 neuropodial acicula are distinct from *A. endonata* which has only one neuropodial aciculum. The specimens of *Arabella iricolor* reported by Hartman (1968) in *Diopatra ornata* are unfortunately no longer available. Hooded setae characteristic of *Arabella mutans* (Chamberlin) and transverse rows of fine teeth on the setae of *A. pectinata* (Fauchald) are key features not found in *A. endonata*. In addition all of the aforementioned species differ significantly in their maxillary formulae.

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I wish to thank Kristian Fauchald and Russel Zimmer for their assistance in preparing the manuscript. A

special thanks to Walter Hoffman and Richard Tibby for making possible the collecting trip to the Port Hueneme area.

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DESCRIPTIONS OF TWO NEW SPECIES OF *EUSCHOENGASTIA* (ACARINA: TROMBICULIDAE) FROM CALIFORNIA AND BAJA CALIFORNIA NORTE, MEXICO

WILLIAM J. WRENN¹ AND RONALD E. SOMERBY²

ABSTRACT: Two new species of *Euschoengastia* are described: *E. hardyorum* n. sp., off *Dipodomys microps* from Death Valley National Monument, 4 mi E Wildrose Ranger Station, Inyo Co, California, and *E. marginalis* n. sp., off *Neotoma lepida* from Lower Covington Flat in Joshua Tree National Monument, Riverside Co, California. Included is information on host-chigger relationships, ecology, seasonal occurrence, and distribution of both species.

Concentrated studies of North American *Euschoengastia* have revealed two new species which are described below. One has been taken only from heteromyid rodents in Inyo County, California, and is similar to *E. romola*, described by Brennan and Jones (Wasmann J. Biol., 12:155-194, 1954) from Monterey County, California. The second resembles several other western species of *Euschoengastia* and usually was found on *Neotoma lepida* from northern Baja California del Norte, Mexico, northward into Inyo County, California. Both species were initially described in an unpublished masters thesis submitted to California State University, Long Beach, by R. E. Somerby entitled "Chiggers of the Genus *Euschoengastia* (Acarina, Trombiculidae) from Southern California," ix + 141 pp., June 1966, and are reinterpreted here.

The holotype and one paratype of each species will be deposited in the collection of the Rocky Mountain Laboratory, Hamilton, Montana. Additional paratypes will be deposited in appropriate collections; other paratypes and specimens examined are in the chigger research collection at California State University, Long Beach, California.

The descriptions of the new species are based upon the holotype, paratypes, and other specimens examined. All measurements are in microns.

Under specimens examined, the enumeration in parentheses following a host name or collection date refers to the number of larvae examined; the second enumeration following the slash refers to the number of hosts examined: (7) or (17/2).

Euschoengastia hardyorum, new species

Figure 1

Types: Larvae, holotype and 48 paratypes from Death Valley National Monument, 4 mi E Wildrose Ranger Station, Inyo Co, California; holotype and two paratypes from *Dipodomys microps*, original number RBL621105-12, collected by Ross Hardy on 2 November 1962 (R. B. Loomis, cataloger); 38 paratypes from nine *Dipodomys microps* (RBL621105-3,-4,-5,-6,-7,-8,-10,-11,-13); and eight paratypes from two *Perognathus formosus* (RBL621105-1,-2), same locality, date, and collector as above.

Diagnosis: ALs < PLs; palpotibial claw pentafurcate; 2 genualae I, without subterminala I, parasubterminala I, genuala III and tibiala III; all dorsal body setae with large conspicuous ventrolateral setules and shorter dorsal setules.

Description of holotype (unless otherwise noted, averages and extremes of 11 paratypes in parentheses).

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² California Dept. Food and Agriculture, Sacramento, California 95814.

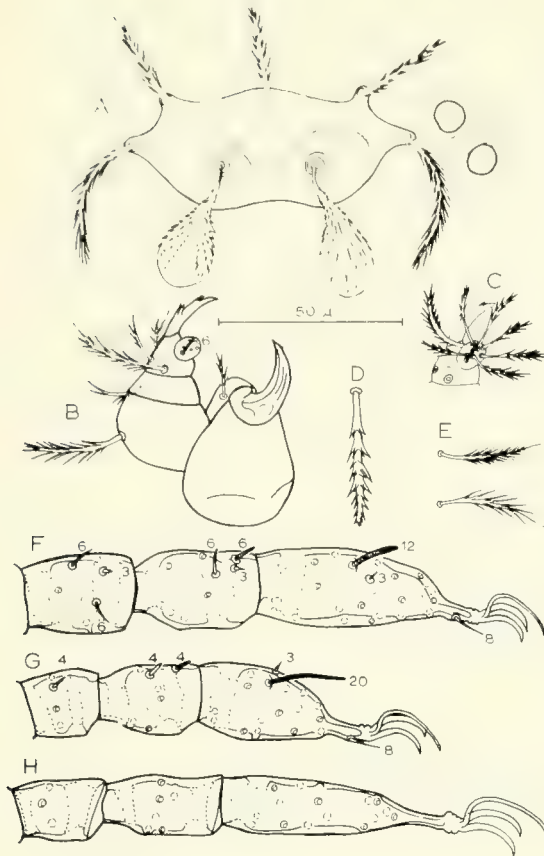


Figure 1. *Euschoengastia hardyorum*, new species: A, scutum; B, ventral aspect of gnathosoma; C, ventral aspect of palpal tibia and tarsus; D, posterodorsal body seta; E, leg setae, typical of distal segments; F, distal segments of leg I with bases of branched and specialized setae (measurements in microns); G, leg II, as above; H, leg III, as above.

theses): Body, engorged, length 416, width 285, color in life white. Eyes 2/2, without ocular plate. Dorsal setae 2-10-10-2-8-6-2, total 40; measurements of humeral seta 39 (40.7, 38-43); anterodorsal 36; posterodorsal 30; shafts of setae in last three rows slightly flattened and expanded; all dorsal setae with large conspicuous ventrolateral setules and smaller dorsal setules. Ventral setae 2-2+34, total 38; measurements of first sternal seta 36; preanal 23; postero-ventral 29.

Scutum.—With flared anterolateral and posterolateral margins, SBs posterior to PLs, prominent ridges anterior to SBs, few scattered inconspicuous puncta; sensilla clavate, anterior surface with long, slender setules becoming sparser distally, posterior aspect with short, blunt setules and a bare median strip becoming wider distally, pedicel with barbs on distal third. Scutal measurements of holotype: AW,

52 (50.8, 48-58); PW, 70 (71.9, 66-81); SB, 26 (26.3, 24-31); ASB, 20 (19.9, 19-21); PSB, 12 (16.6, 9-13); AP, 16 (14.1, 12-16); AM, 27 (25.6, 24-27, eight paratypes); AL, 28 (29.1, 27-32); PL, 37 (42.4, 41-45); SL, 36 (34, 32-36, eight paratypes); SW, 14 (14.6, 13-16, nine paratypes).

Gnathosoma.—Galeala with four branches (3 to 4-branched). Palpal formula B/B/BBB; palpotibial claw pentafurcate; lateral palpotibial seta with three branches (2 to 3-branched). Cheliceral bases without puncta.

Legs.—Subterminala I, parasubterminala I, genuala III and tibiala III absent; tarsi of legs I, II, and III with 23, 16, and 15 setae, respectively. Leg index of holotype: I, 244; II, 206; III, 241; total, 691. Mean and range of selected nude setae of 11 paratypes: tarsala I, 12.9, 12-14; tarsala II, 19.9, 19-21; proximal tibiala I, 7, 6-9; distal tibiala I, 7, 6-9; proximal tibiala II, 4.5, 4-5; distal tibiala II, 4.8, 4-6; dorsal genuala I, 6.3, 5-9; posteroventral genuala I, 6.4, 6-9; genuala III, 4.6, 4-6. Coxae and other leg segments not punctate.

Specimens examined (74 larvae): CALIFORNIA. Inyo Co: Death Valley National Monument, 4 mi E Wildrose Ranger Station (5710 ft), 2 November 1962, 10 *Dipodomys microps* (41), two *Perognathus formosus* (8); 5 mi E Wildrose Ranger Station, 8 September 1962, *P. formosus* (3); Argus Mts., Home-wood Canyon, Ruth Mine (3860 ft), 8 November 1964, *Thomomys umbrinus* (1), *Dipodomys merriami* (3), three *P. formosus* (18).

Taxonomic remarks: *Euschoengastia hardyorum* is similar to *E. romola* Brennan and Jones in lacking subterminala I, genuala III and tibiala III, and in overall size. It differs from *E. romola* in having a pentafurcate palpotibial claw, the posterior two or three rows of dorsal body setae are slightly expanded, and all dorsal body setae have large conspicuous ventrolateral setules (*E. romola* has a trifurcate palpotibial claw, all dorsal body setae, except the medial-most of the first posthumeral row, are flattened and appear leaf-like, with small ventrolateral setules similar to the dorsal setules).

Euschoengastia hardyorum is named for Ross Hardy and his son, Alan Hardy, formerly of California State University, Long Beach, in recognition for their many contributions of mammals which were examined for ectoparasites.

Ecological notes: The type locality in Wildrose Valley was on an alluvial fan which extended from the mouth of Upper Wildrose Canyon. The area was covered by a desert pavement of coarse gravel between larger rocks. The most common plant was blackbrush, *Coleogyne ramosissima* Torrey. The whitish-colored larvae were in pits on the venter (belly, legs, and genital area) of heteromyid

rodents trapped in early September and early November.

***Euschoengastia marginalis*, new species**

Figure 2

Types: Larvae, holotype and 15 paratypes from Joshua Tree National Monument, Lower Covington Flat, Riverside Co, California, collected 19 February 1961 by Dennis G. Rainey; holotype and seven paratypes from *Neotoma lepida*, original number KDP610314-7 (K. D. Peyton, cataloger); seven paratypes from *Perognathus fallax* (KDP610314-6); and one paratype from *Dipodomys merriami* (KDP610314-8).

Diagnosis: ALs and PLs subequal, sensillary head capitate, pedicel distinct; palpotibial claw trifurcate, lateral palpotibial seta nude (sometimes with 1 or 2 small branches); microgenuala I and microtibiala I dagger-like (short, thick), subterminala I and parasubterminala I present, tibiala III absent; all dorsal body setae with long, conspicuous ventrolateral setules and shorter dorsal setules.

Description of holotype (differences in specimens from throughout the range noted in parentheses): Body, slightly engorged, length 264, width 175, color in life orange. Eyes 2/2, without ocular plate. Dorsal setae 2-12-12-9-8-6-6, total 55, with long, conspicuous ventrolateral setules and shorter dorsal setules; first and second posthumeral rows usually with 12 setae (of 53: 3 percent with 10, 15 percent with 11, 69 percent with 12, 12 percent with 13, 2 percent with 14); measurements of humeral seta 42; anterodorsal 42, posterodorsal 38. Ventral setae 2-2+57, total 61; measurements of first sternal seta 43; preanal 23, posteroventral 30.

Scutum.—With few, conspicuous puncta, bases SBs slightly posterior to bases PLs, prominent ridges anterior to SBs; sensillae capitate, posterodistal median area bare, pedicel distinct; scutal setae densely covered with setules. Scutal measurements of holotype followed by measurements of specimens from throughout the range (mean, range, and sample size): AW, 53 (52, 45-59, 52); PW, 72 (73.4, 66-79, 57); SB, 15 (19.7, 15-28, 59); ASB, 29 (27.6, 18-30, 58); PSB, 14 (15.4, 11-20, 58); AP, 21 (21.5, 18-26, 59); AM, 30 (31.2, 27-35, 48); AL, 45 (43, 38-51, 56); PL, 43 (43.6, 39-48, 57); SL, 29 (30.6, 27-35, 24); SW, 18 (19.1, 17-21, 44).

Gnathosoma.—Galeala branched. Palpal formula B, B BNB; palpotibial claw trifurcate; lateral palpotibial seta nude (of 30 from Joshua Tree National Monument: 77 percent nude, 23 percent forked to 3-branched). Cheliceral bases and palpal coxa with few, inconspicuous puncta.

Legs.—Tarsi of legs I, II, and III with 22, 16, and 15 setae, respectively. Leg index of holotype: I, 265; II, 223; III, 245; total, 733. Measurements and positions of nude setae as in figure 2. Mean, range,



Figure 2. *Euschoengastia marginalis*, new species: A, scutum; B, ventral aspect of gnathosoma; C, ventral aspect of palpal tibia and tarsus; D, coxa III; E, anterodorsal body seta; F, distal segments of leg I; G, leg II, as above; H, leg III, as above; I, leg setae, typical of distal segments.

and sample size of selected setae of specimens from throughout the range: subterminala I, 16.9, 15-21, 55; parasubterminala I, 10.6, 9-12, 39; tarsala I, 15.9, 14-19, 57; tarsala II, 19.8, 17-21, 57; proximal tibiala I, 11.9, 10-16, 56; distal tibiala I, 10.9, 9-14, 56; proximal tibiala II, 6.9, 6-11, 57; distal tibiala II, 7, 5-12, 56; dorsal genuala I, 9.9, 7-16, 50; posteroventral genuala I, 11.2, 9-18, 47; genuala II, 5.5, 5-7, 57; genuala III, 5.4, 5-9, 52. Coxae conspicuously punctate; other leg segments with few, inconspicuous puncta.

Specimens examined (645 larvae): MEXICO. *Baja California Norte*: 4 mi S El Topo, 29 December 1962, two *Neotoma fuscipes* (12), *Neotoma lepida* (7), *Perognathus californicus* (2). CALIFORNIA. *Inyo Co*: Death Valley National Monument, Eagle Borax Works ruins, 21 December 1962, *Peromyscus eremicus* (1). *San Diego Co*: 5 mi E, 5 mi S Pine Valley, 5 November 1961, *N. fuscipes* (20). *Kern Co*: 10 mi NNW Mohave, 3 November 1968, *Dipodomys panamintinus* (1). *San Bernardino Co*: 8 mi S

Barstow, 26 January 1963, *Neotoma lepida* (8); 12 mi S Needles, 6 February 1965, three *N. lepida* (6); 1.2 mi N Yucca Valley, 23 November 1963, three *N. lepida* (20); 1.5 mi W Yucca Valley, 8 November 1963, *N. lepida* (3); the following from Joshua Tree National Monument: Long Cyn. (4.8 mi N of south boundary of Monument), 17 March–28 April 1963, *P. eremicus* (1), three *N. lepida* (7); Indian Cove (3000–3500 ft), three *N. lepida*, 22 January 1961 (10), 4 March 1962 (2), 26 November 1967 (5), two *P. eremicus*, 22 January 1961 (1), 26 November 1967 (2); Lower Covington Flat (4200–4700 ft), 16 *N. lepida*, 29 November 1959 (17/2), 22 February 1960 (79/6), 22 January 1961 (76/5), 10 February 1962 (7/2), 16 December 1963 (7), *Perognathus fallax*, 22 February 1960 (4). *Riverside Co.*: all from Joshua Tree National Monument; 2.2–3.5 mi S Cottonwood Spring, three *N. lepida*, 23 January 1961 (1), 28 January 1962 (22/2); 1.7 mi SSW Cottonwood Spring, 5 February 1967, two *N. lepida* (3), three *P. fallax* (10); Long Cyn., 16–17 February 1963, three *N. lepida* (20), 2–16 March 1963, two *N. lepida* (14), *Dipodomys merriami* (1), two *P. fallax* (5); Lost Horse Valley, 29 December 1961, two *N. lepida* (20), 9–10 February 1962, four *N. lepida* (18), *Peromyscus truei* (1), 21 December 1963, *N. lepida* (8), *P. fallax* (1); Lower Covington Flat, six *N. lepida*, 29 November 1959 (14), 20 March 1960 (16), 19 February 1961 (16), 20 October 1962 (9), 16 December 1963 (15/2), *D. merriami*, 19 February 1961 (1), *P. fallax*, 19 February 1961 (7); Upper Covington Flat, 28 November 1959, *N. fuscipes* (1); 2 mi NW Old Dale Junction, 9 December 1962, *N. fuscipes* (4); Pinyon Wells, 18 March 1962, two *N. lepida* (10); Squaw Tank, 11 *N. lepida*, 28 December 1961 (44/4), 9 February 1962 (17/3), 24 February 1963 (20/3), 8 December 1963 (6), *D. merriami*, 9 February 1962 (8), *P. fallax*, 9 February 1962 (1); Stubby Springs, two *P. fallax*, 4 April 1969 (8), 30 March 1969 (4); White Tank, 25 February 1961, six *N. lepida* (29), *D. merriami* (1).

Taxonomic remarks: *Euschoengastia marginalis* is similar to *E. ambocalis* Wrenn and Loomis (J. Med. Ent., 10:97–100, 1973), *E. fasolla* (Gr. Basin Nat., 15:1–26, 1956), and *E. radfordi* Brennan and Jones (1954) in having the AL and PL setae subequal and capitate sensillae with distinct pedicels. It differs from *E. ambocalis* in having long, conspicuous ventrolateral setules on all dorsal body setae and a nude lateral palpotibial seta (setules subequal and a branched palpotibial seta in *E. ambocalis*); from *E. fasolla* by the presence of a subterminala I and a parsubter-

terminala I (absent in *E. fasolla*); and from *E. radfordi* in having a dagger-shaped microgenuala I and microtibiala I, and inconspicuous puncta on the cheliceral bases and distal leg segments (needle-shaped and strongly punctate in *E. radfordi*). The average lengths of certain nude leg setae of larvae from San Diego County and Baja California del Norte were slightly longer (up to 5 microns) than those of specimens from Riverside and San Bernardino counties; for example, posteroventral genuala I, 16 versus 10.3, and proximal tibiala I, 13.7 versus 11.6. The populations were similar in other respects.

Ecological notes: Larvae were recorded from 101 individual hosts; 74 were *Neotoma lepida*; the other 27 hosts included three species of cricetids and four of heteromyids which usually were taken from the same trap lines as *N. lepida*. Known localities for *E. marginalis* are generally habitats at the margins of deserts and the dry coast. The orange-colored larvae were found deep in the external auditory meatus of hosts from mid-October through April; however, the highest incidence extended from November through March.

ACKNOWLEDGMENTS

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We express our gratitude to the many faculty and students, presently or formerly, at California State University, Long Beach, who provided host mammals and their chiggers, especially Ross Hardy, Dennis G. Rainey, Kenneth D. Peyton, Richard M. Davis, Lynell K. Tanigoshi, Robert C. Stephens, H. Stephen Logsdon, Elbert L. Sleeper, Alan Hardy, and Dean E. Harvey. We appreciate the issuance of collecting permits from officials for California, Death Valley and Joshua Tree National Monuments and Mexico.

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THE CHELICERAL MUSCLES OF THE SCORPION *HETEROMETRUS FULVIPES*

A. B. VYAS¹

ABSTRACT: The movements of a scorpion chelicera are brought about by eighteen muscles. Observations on the origin, insertion, and action of each of these muscles have been recorded.

The distal segments of the scorpion chelicerae are modified as pincers which handle prey, including piercing the body so that nutrient fluids may be extracted. While a number of workers such as Cloudsley-Thompson (1958), Stahnke (1966), and Venkateshwararao (1967) have pointed out the role of the chelicerae in feeding, the muscles which operate these appendages have not received much attention. Literature on the myology of scorpions includes contributions of Lankester, Benham, and Beck (1885), Snodgrass (1952), and Dubale and Vyas (1967, 1968, 1969), but throws only little light on the myology of the chelicera. Therefore a study of musculature of the chelicerae was undertaken.

METHODS

The Indian ground scorpion *Heterometrus fulvipes* was utilised. Specimens were mostly collected from uncultivated land around the Gujarat University Campus, Ahmedabad. The muscles were studied by dissection with the aid of a stereoscopic microscope. The action of each individual muscle was demonstrated mainly by electrical stimulation. For this purpose the dissections were performed upon living specimens in scorpion-Ringer solution. A nine-volt transistor cell battery was used as a source of the stimulus. The drawings showing the disposition of the various muscles and the arrangement of muscle fibres were made from the dissections.

OBSERVATIONS

The chelicerae of the scorpion *Heterometrus fulvipes* resemble those of other scorpions described by Lankester, *et al.*, (1885), Snodgrass (1952), and Awati and Tembe (1956) and comprise three segments. The basal segment is known as the coxa; the second and the terminal segments are termed respectively the deutomerite and the movable finger.

The coxa is annular with a long process, called the coxal entosclerite, which extends backwards and gradually tapers towards the free end. On the coxal entosclerite are attached many of the cheliceral muscles.

The swollen barrel-shaped deutomerite is the largest segment. Its ventro-medial edge is provided with a brush of long stout hairs called the "dermatothecatae plerothaeate" (Pawlowsky, 1924). The digitiform inner distal portion of this segment, known as the immovable finger, bears a number of stout chitinous teeth.

The terminal segment arises from the distolateral portion of the deutomerite, with which it is articulated by a hinge joint. This segment also bears strong teeth along its inner margin. Thus the movable and immovable fingers combined form a powerful nipping organ called the chela of the chelicera.

The coxal joint which connects the coxa with the body consists entirely of a pleural membrane and allows free movement of the chelicera in various directions. The joint between the coxa and the deutomerite consists of a narrow circular corium and permits only limited promotory and remotary action of the deutomerite. The hinge joining the movable finger to the deutomerite allows only adduction and abduction of the movable finger.

MUSCLES OF THE CHELICERA

The cheliceral muscles like those in other arthropodan appendages can be divided into two main categories: extrinsic and intrinsic. While the former muscles arise from outside the appendage and are mainly concerned with its movement as a whole, the latter originate and insert within the respective segments and affect the movements of the different parts of the appendage.

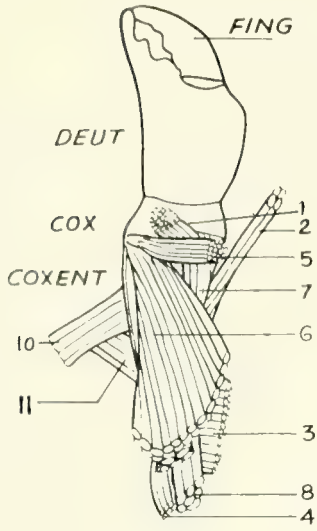
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TABLE 1. Classification and anatomical arrangement of cheliceral muscles of the Indian ground scorpion. The number in parentheses is used in the discussion and description to identify a particular muscle. B = broad; F = fleshy; N = narrow; T = tendinous.

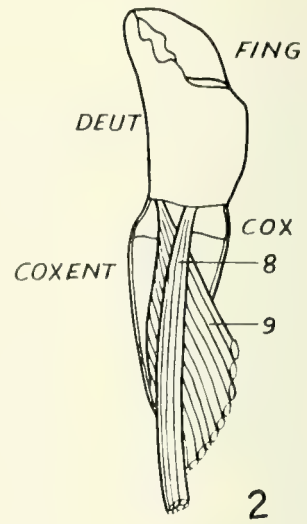
Muscle	Nature: shape, structure, arrangement of muscle fibers	Origin	Insertion	Function
EXTRINSIC MUSCLES				
<i>Dorsocoxal entosclerite muscles</i>				
(1) Superior dorsocoxal entosclerite	Small, obliquely placed, pinnate	B, F, anteromedian region of carapace	N, T, outer margin of the coxal entosclerite	Rotates chelicera inward
(2) Anterior dorsocoxal entosclerite	Thin, ribbon-shaped, pinnate	F, anterolaterally from carapace	T, posterolateral on coxal entosclerite	Produces forward movement of the appendage
(3) Lateral dorsocoxal entosclerite	Thin, ribbon-shaped horizontal parallel towards insertion runs below coxal entosclerite	F, anterolateral from carapace	Tonofibrillar, inner margin of the coxal entosclerite	Adduction of chelicera
(4) Posterior dorsocoxal entosclerite	T, cylindrical pinnate	F, posterior portion of carapace	T, posterior end of coxal entosclerite	Remotion of chelicera
(5) Superior dorsocoxal	Horizontal and twisted, pinnate	<i>Dorsocoxal muscles</i>		
(6) Interior dorsocoxal	Fan-shaped pinnate	F, B, anterolateral portion of carapace	N, T, inner dorsal base of coxa	Outward rotator of chelicera
(7) Exterior dorsocoxal	Ribbon-shaped, elongated, F, parallel	B, F, anterolateral region of carapace	T, on inner dorsal base of coxa, remain covered by (5)	Adduction of coxa as well as whole appendage
(8) Superior dorsodeutomerite	F, long, cylindrical run parallel to (7) pinnate	Midlateral region of carapace	Base of coxa, remain covered with (5)	Outward movement of chelicera and/or coxa
(9) Inferior dorsodeutomerite	B, F, fan-shaped fills major space of coxal entosclerite covered with (7) and (8)	<i>Dorso-deutomerite muscles</i>		
		F, carapace interior to that of (7)	T, middorsal rim of deutomerite	Remotor of deutomerite
		B, F, posterior to (7) and (8)	N, T, dorsal base of deutomerite	Flexor of deutomerite (bends inwards)
(10) Anterior coxal entosclerite-preoral entosclerite	B, thin ribbon-shaped, ventrally provided with a tendinous sheet, parallel	<i>Coxal entosclerite-preoral entosclerite muscles</i>		
		B, F, preoral entosclerite	T, anterior part of the coxal entosclerite	Powerful adductor of chelicera

TABLE 1. (Continued)

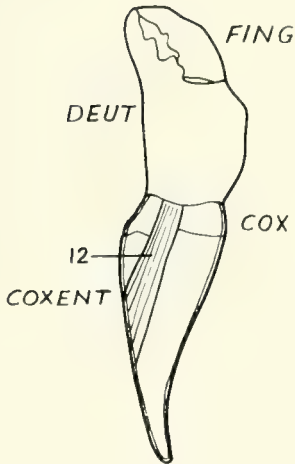
Muscle	Nature: shape, structure, arrangement of muscle fibers	Origin	Insertion	Function
(11) Posterior coxal entosclerite-preoral entosclerite	B, thin ribbon-shaped, ventrally provided with a tendinous sheet, parallel	B, F, remains covered with (10)	T, inner posterior border of coxal entosclerite	Abductor of chelicera
<i>Coxal entosclerite deutomerite muscles</i>				
(12) Interior coxal entosclerite deutomerite	Fan-shaped, remain covered with (6), pinnate	B, F, inner margin of coxal entosclerite	N, tonofibrillar, middorsal base of deutomerite	Backward movement of deutomerite
(13) Exterior coxal entosclerite deutomerite	B, F, thin, fanlike, closely applied to ventral wall of coxal entosclerite, covered with extrinsic muscles	B, F, ventral wall of coxal entosclerite runs through coxa	N, T, ventral base of deutomerite	Depressor of deutomerite
INTRINSIC MUSCLE				
<i>Coxa-deutomerite muscles</i>				
(14) Superior coxal deutomerite	F, smallest pinnate	B, F, inner dorsal wall of coxa	Tonofibrillar, inner dorsal base of deutomerite	Forward movement (pro-motion) of deutomerite
(15) Inferior coxal deutomerite	F, outer part of coxal cavity, pinnate	B, F, partly covered with (14)	N, T, middorsal base of deutomerite	Inward rotator of deutomerite
(16) Exterior coxal deutomerite	F, cylindrical, opposite to (15) horizontal and twisted, pinnate	N, F, outer lateral wall of coxa	N, T, ventral margin of deutomerite remains covered with (15)	Outward rotator of deutomerite
(17) Adductor	F, large and massive, fills major space in deutomerite, pinnate	<i>Muscle operating movable finger</i> B, F, dorsal, inner and ventral walls of deutomerite		
				Powerful adductor of movable finger (help closing of pincer)
(18) Abductor	Small, T, pinnate	N, T, outer wall of deutomerite	N, T, base of movable finger, N	Abductor of movable finger



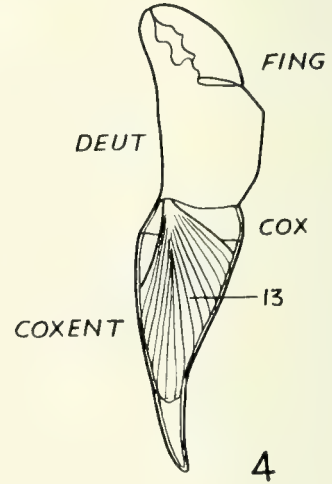
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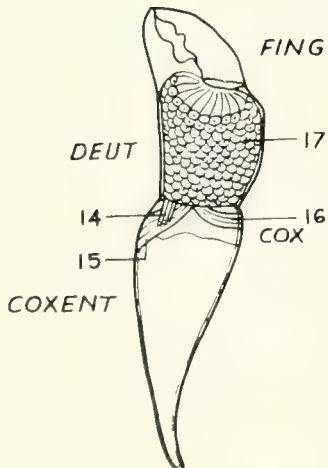
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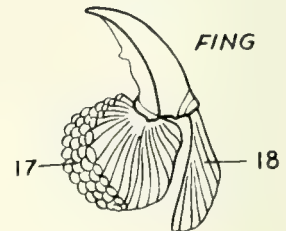
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6

An outline of the classification and anatomical arrangement of the scorpion cheliceral muscles is given in table 1 and figures 1-6. Each muscle has been given a number (shown in the parentheses) which is used in the discussion and description to avoid lengthy nomenclature.

DISCUSSION

Scorpions are predaceous and extract juices from prey (Brunson, 1951; Stahnke, 1966). The role of chelicerae in feeding can be clearly understood from the work of Stahnke (1966). According to him . . . "The pedipalps move the prey to the chelicerae which are small chelate appendages, their shearing jaws are used to pierce, cut and tear the soft and hard parts of the prey into minute pieces. . . . The tiny particles produced by the chelicera are packed between the coxa of the pedipalps." All these actions necessitate a free movement of these appendages in various directions.

A casual study of the arthrology of the chelicera revealed that the coxal joint simply consists of arthrodial membrane and allows great freedom of movement.

The adduction is brought about by three muscles, viz. (10), (3), and (6). The first two muscles are broad and with parallel fibers, whereas, the last is fan-shaped and exhibits pinnate structure. All these muscles are well-developed and powerful. Although they arise from different regions of the prosoma, their contraction results in an inward movement of the chelate end of the appendage.

The muscles (11) and (7) serve as abductors. Their contraction moves ends of the two chelicerae apart. Both these muscles are well-developed with parallel fibers.

Inward and outward rotatory movements of the chelicerae are brought about respectively by (1) and (5) muscles. These muscles are relatively small but their pinnate nature suggests powerful action.

The promotory and remotory movements of these appendages are brought about by the (2)

and (4) muscles, respectively. Both these muscles are narrow and tendinous.

An inward flexion at the joint between the coxa and deutomerite segments of the chelicera results from action of the (13) and (9) muscles. These muscles show pinnate arrangement of the muscle fibers and are provided with tendons at their insertion ends. As stated earlier, this joint allows relatively lesser movement and as such requires the presence of powerful muscles for flexor movement. The pinnate nature and the tendinous material of the (13) and (9) muscles are thus suitably adapted to meet these functional demands. The contraction of these muscles enables the animal to bring the chelate organ of its chelicerae much closer to the mouth. The muscle operating the extensor mechanism of these segments is relatively weak in action.

A noteworthy feature of the muscles operating the chela of the chelicerae is that unlike the condition in scorpion pedipalps, both adductor and abductor sets of muscles are represented (Snodgrass, 1952). Compared with the abductor muscle (18), the adductor (17) is powerful.

ACKNOWLEDGMENTS

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Figure 1. Extrinsic muscles of chelicera (Dorsal view). Figure 2. Dorso deutomerite muscles (other muscles removed). Figures 3 and 4. Intrinsic muscles of coxal entosclerite. Figures 5 and 6. Intrinsic muscles of coxa and deutomerite segments. COX = Coxa. COXENT = Coxal entosclerite; DEUT = Deutomerite segment; FING = Movable finger. For identification of numbered muscles see table 1.

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XIPHIORHYNCHUS KIMBLALOCKI, A NEW BILLFISH FROM THE EOCENE OF MISSISSIPPI WITH REMARKS ON THE SYSTEMATICS OF XIPHIROID FISHES

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ABSTRACT: *Xiphiorhynchus kimblalocki*, a new species of extinct billfish from the Eocene of Mississippi, is described. This is the first record of *Xiphiorhynchus* outside of western Europe, and the material consists of a well-preserved rostrum, three partial vertebrae and two fin spine fragments. *Xiphiorhynchus kimblalocki* is compared with other living and extinct billfish and appears to be intermediate in morphology between the Xiphiidae and Istiophoridae. Various genera of fossil billfish are critically discussed and we suggest that the Blochiidae, Paleorhynchidae, and the "*Cylindracanthus*-group" should be placed in Xiphioidae *Incertae sedis* until better evidence indicates that they are billfish. We speculate that *Xiphiorhynchus* is an extinct offshoot from an unknown pre-Eocene common ancestor between Xiphiidae and Istiophoridae and is closer to the Istiophoridae than to the Xiphiidae. We also agree with earlier workers that the lineages of the Xiphiidae and Istiophoridae run back separately into basal Eocene times and that any common ancestry to each other and to the scombroids must have been prior to the Eocene and may have extended into the Cretaceous.

Billfish remains have been described in rocks from the Cretaceous Age (Dixon, 1850) to the Pleistocene (Fierstine and Applegate, 1968). The exact taxon to which many of these remains belong has puzzled paleontologists because identifications are usually based on isolated skeletal parts, particularly the rostrum. Detailed anatomical comparisons of recent genera are lacking and the lack of information has led to nomenclatorial confusion and misidentification of the fossil forms. Various attempts have been made to synthesize the avail-

able evidence and to make order out of chaos (Woodward, 1901; Leriche, 1905; Carter, 1927; Casier, 1946, 1966). Unfortunately, even the

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latest monograph (Casier, 1966) has failed to apply the well-established nomenclature and biological knowledge used by recent ichthyologists (Greenwood, Rosen, Weitzman, and Myers, 1966; Gosline, 1968; Howard and Ueyanagi, 1965; Morrow and Harbo, 1969; Nakamura, Iwai, and Matsubara, 1968; Robins and de Sylva, 1960, 1963). Thus, it is the object of this paper to describe a new species from the Eocene of Mississippi and to put at least a part of the fossil billfish problem in a more modern perspective.

SYSTEMATIC DESCRIPTION

CLASS OSTEICHTHYES

Order Perciformes

Suborder Xiphioidae

Family Xiphiorhynchidae

Genus *Xiphiorhynchus*, Van Benden, 1871

Xiphiorhynchus kimblalocki, new species Figures 1-4

Holotype: LACM 25575.1, a rostrum (Figs. 1, 2); LACM 25575.2, a partial anterior abdominal vertebra (Fig. 3); LACM 25575.3, a partial posterior caudal vertebra (Fig. 3); LACM 25575.4, a vertebral frag-

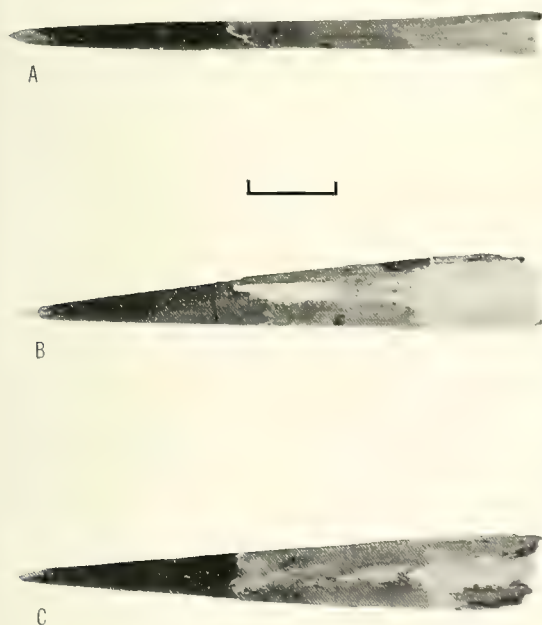


Figure 1. Rostrum of *Xiphiorhynchus kimblalocki*, new species (Holotype—LACM 25575.1): A. lateral view; B. ventral view; C. dorsal view. Scale equals 10 cm.

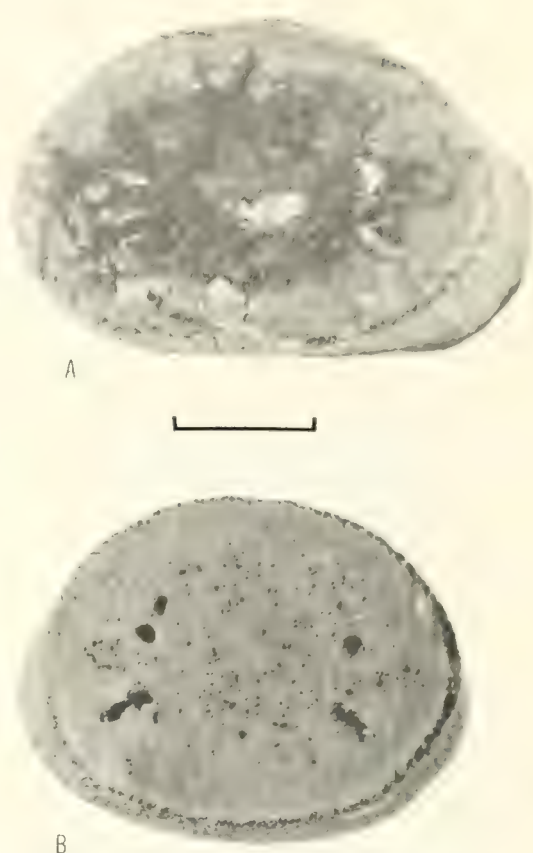


Figure 2. Rostrum of *Xiphiorhynchus kimblalocki*, new species (Holotype—LACM 25575.1): A. cross-section 220 mm from distal tip; B. cross-section 170 mm from distal tip. Scale equals 15 mm.

ment; LACM 25575.5, a partial fin spine (Fig. 4); LACM 25575.6, a partial fin spine (unfigured).

Horizon and Locality: LACM locality 7003, Scott Co., Mississippi. Southwest side of Sherman Hill (Hill 618), NW $\frac{1}{4}$ SW $\frac{1}{4}$ Sec 16, T5N, R9E, Forest (?Hill) Quadrangle, U.S.G.S., 1950. The specimens were collected in the Shubuta Clay member of the Yazoo Formation, Jackson Group (Eocene). The Shubuta consists of green to greenish-gray calcareous to non-calcareous, glauconitic, fossiliferous, silty clays (DeVries, *et al.*, 1963). Selenite crystals are common. There is no indication that the fossil was collected near the base or near the top of the formation. The associated fauna consisted of a skull and cervical vertebrae of *Zygorhiza kochi*, an extinct, primitive cetacean.

The species is named in honor of Mr. Kim Blalock who collected the specimens and discovered the site.

Diagnosis: The rostrum differs from other *Xiphiorhynchus* in its large size, rugose surface texture, lack of a central longitudinal nutrient canal at its distal end, and its diminutive alveoli.

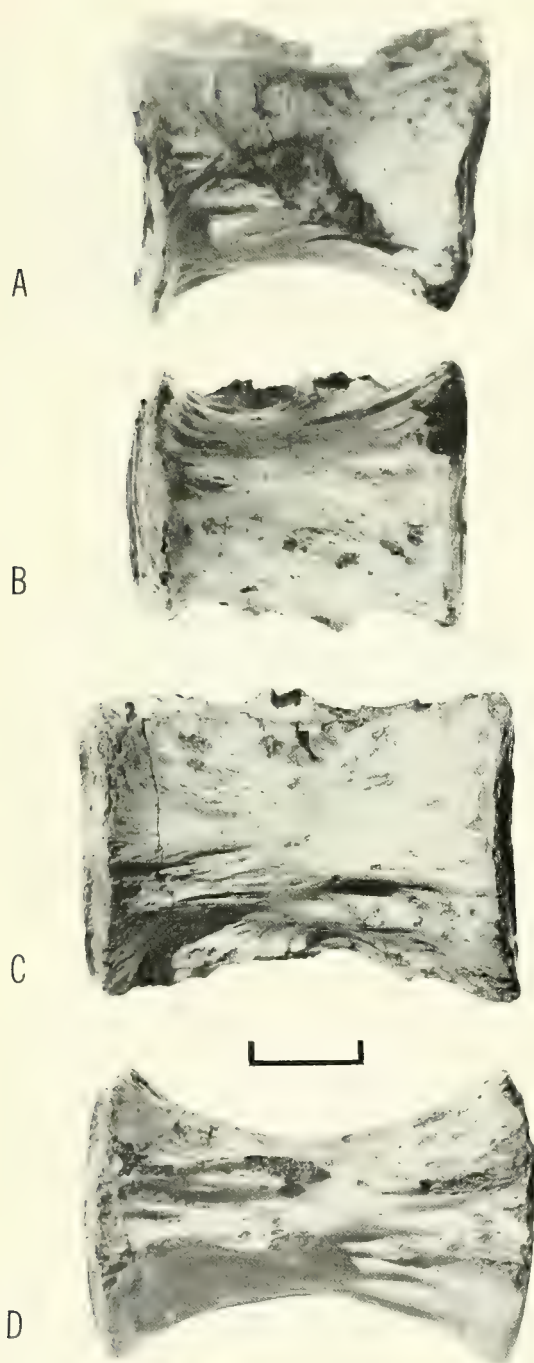


Figure 3. Vertebrae of *Xiphiorhynchus kimblalocki*, new species (Holotype): A. partial abdominal vertebra (LACM 25575.2), lateral view; B. partial abdominal vertebra (LACM 25575.2), ventral view; C. partial caudal vertebra (LACM 25575.3), lateral view; D. partial caudal vertebra (LACM 25575.3), ventral view. Scale equals 25 mm.

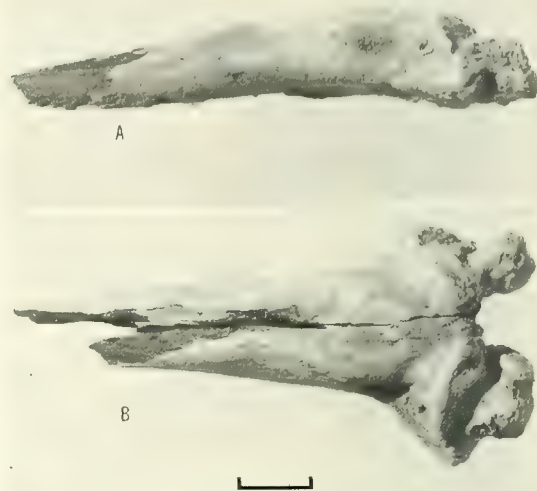


Figure 4. Fin spine of *Xiphiorhynchus kimblalocki*, new species (Holotype—LACM 25575.5): A. lateral view; B. anterior view. Scale equals 10 mm.

Description: The greatest length of the rostrum is 580 mm; it is nearly circular in cross-section at its distal tip and it becomes progressively larger and more depressed in cross-section towards its proximal end. One centimeter from the distal tip, the rostrum measures 11 mm wide and 12 mm thick, and the proximal end (base) is 83.5 mm wide and 38.0 mm thick. The proximal one-half probably was slightly depressed and crushed during preservation.

The dorsal surface is rugose at its distal end and longitudinally striated at its proximal end. Ventrally, the distal one-half is rugose. A poorly preserved alveolar layer covers the middle one-half of the ventral surface of the rostrum. The alveoli range from .25 to .4 mm in diameter. The proximal one-fourth of the ventral surface is not preserved.

A cross-section of the rostrum (Fig. 2), cut 220 mm from the distal tip, revealed poorly preserved bone. Traces of matrix revealed a central longitudinal nutrient canal which is bordered laterally by a pair of smaller lateral longitudinal nutrient canals.

A cross-section of the rostrum 170 mm from the distal tip (Fig. 2) revealed three right lateral longitudinal nutrient canals and two left lateral longitudinal nutrient canals. The central longitudinal nutrient canal had terminated prior to this section.

The centrum (Fig. 3) of the anterior abdominal vertebra (LACM 25575.2) is 70 mm long and the anterior and posterior surfaces are nearly circular.

The ratio of the height (60.4 mm) of the centrum, measured at its anterior surface, to its greatest length (70.0 mm) is 0.86. The surface texture is rugose and contains many pits and fossae. In lateral view, the ventral surface is gently concave; in ventral view the lateral surfaces are relatively flat and do not have a "pinched-in" appearance. The neural arch is broken at its base, but appears to be divided into a larger anterior zygopophysis and a smaller posterior zygopophysis. A large rib attachment area is present on each lateral side.

The centrum (Fig. 3) of the posterior caudal vertebra (LACM 25575.3) is 92.5 mm long and the anterior and posterior surfaces are nearly circular. The ratio of the height (64 mm) of the centrum, measured at its posterior surface, to its greatest length (92.5 mm) is 0.69. The surface texture is rugose and contains many pits and fossae. In lateral view, the ventral surface is gently concave; in ventral view, the lateral surfaces are concave and present an hourglass outline. The zygopophyses and the neural and haemal arches are broken off at their bases.

The two partial fin spines (LACM 25575.5 and LACM 25575.6) belong to a median (anal or dorsal) fin (Fig. 4). LACM 25575.5 measures 34 mm across its nearly complete base and 72 mm long. Although its distal tip is missing, it appears to have tapered rapidly to a point. When viewed from the side, it shows a slight posterior curvature. If the spine had been complete, we estimate that it would have measured 112 mm long and 40 mm wide. LACM 25575.6 is a left or right half of a spine that measures 20 mm across its base and 138 mm in length. When viewed from the side, it shows no antero-posterior curvature. If the spine had been complete, we estimate it would have measured 40 mm across its base and 210 mm in length.

DISCUSSION

The rostrum of *Xiphiorhynchus kimblalocki*, like other species of *Xiphiorhynchus* (Leriche, 1905; Casier, 1966), is similar in morphology to those found in the Istiophoridae (Tables 1 and 2). It differs, however, in the number of nutrient canals (Table 2), in having smaller alveoli, and in having a more depressed cross-section at its base (Table 1). The longitudinal openings, revealed in transverse section (Fig. 2), can be called nutrient canals with some assurance, since histological examination of the rostrum of a striped marlin (*Tetrapturus audax*) revealed blood vessels within the canals (Vladimir Walters, Univ. California, Los Angeles, unpublished).

The rostrum of the swordfish (*Xiphias gladius*), when compared to the rostrum of *X. kimblalocki*,

is more greatly depressed along its entire length. However, measurements taken at the base of the rostrum (Table 1) show that *X. kimblalocki* and *X. gladius* are nearly equally depressed. As noted earlier, some of the depression at the base of the rostrum in *X. kimblalocki* may be due to deformation during preservation. The rostrum of the swordfish lacks alveoli and denticles, but it does contain a central (? nutrient) canal and one pair of lateral nutrient canals.

The rostra of *Blochius* and what we are calling the *Cylindracanthus*-group (*Aglyptorhynchus*, *Congorhynchus*, *Cylindracanthus*, *Glyptorhynchus*, *Hemirhabdorrhynchus*, etc.) are much smaller than the rostra considered above. They all probably have numerous longitudinal nutrient canals (Carter, 1927; Casier, 1966; Fierstine and Applegate, unpublished).

The two vertebrae of *X. kimblalocki* differ from those of other billfish (Table 3). The anterior abdominal vertebra is similar in size and shape to a third or fourth abdominal of a black marlin (*Makaira indica*). It differs, however, in its rugose surface texture (the centrum of the black marlin is relatively smooth), the lack of a fossa on its ventral surface, and the shape and placement of its rib attachment. The third vertebra of the black marlin lacks a pronounced transverse process and has a large oval scar for rib attachment. The transverse process of *X. kimblalocki* is broken at its base, but it probably was large and quite pronounced.

The third vertebra of *X. gladius* has a thin, well-developed transverse process and no obvious rib facet. In this respect, the centrum of *X. gladius* is similar to the centrum of *X. kimblalocki*. The third vertebra of the swordfish (like most other vertebrae in the vertebral column) is more lightly constructed, appears to be more weakly ossified, and the surface architecture is smoother than for the abdominal vertebra of *X. kimblalocki*.

The caudal vertebra of *X. kimblalocki* differs considerably from any istiophorid caudal vertebra. It most closely resembles one from the posterior caudal region (approximately in the vicinity of the 21st vertebra). The height to length ratio of the centrum is much larger than the ratio for the three living istiophorid genera (Table 3). Thus, the caudal vertebra of *X. kimblalocki* is much more cube-like than those found in the Istiophoridae. The height to length ratio of the centrum compares much more favorably with the 21st centrum of *X. gladius*. The probable placement of the neural and haemal spines is similar.

TABLE 1. Height to width ratios of the rostra of certain billfish.

Species	Base	Middle Point	Tip (-1 cm)
<i>Istiophorus platypterus</i> (Sailfish)	$\frac{18}{22} = .82$	$\frac{13.5}{17.5} = .80$	$\frac{8}{11} = .73$
<i>Makaira indica</i> (Black marlin)	$\frac{46.5}{66.0} = .70$	$\frac{36.0}{43.5} = .83$	Missing
<i>Tetrapturus audax</i> (Striped marlin)	$\frac{22}{37.5} = .59$	$\frac{15.0}{22.5} = .67$	$\frac{5.2}{7.2} = .72$
<i>Xiphias gladius</i> (Swordfish)	$\frac{39}{89} = .44$	$\frac{18}{60} = .30$	$\frac{11}{39} = .28$
<i>Xiphiorhynchus kimblalocki</i>	$\frac{38}{83.5} = .46$	$\frac{35.3}{57.0} = .62$	$\frac{11}{12} = .92$

but as with the anterior caudal vertebra, the surface texture and construction is much more rugose and massive in *X. kimblalocki* than in the swordfish.

Casier (1966) described and figured from the London Clay, a vertebra that he identified as *Xiphiorhynchus* (?). This centrum is very similar in shape and preservation to the caudal vertebra of *X. kimblalocki*.

Systematics of the Xiphioid Fishes.—Fierstine and Walters (1968) and Gosline (1968) independently concluded that the Istiophoridae and Xiphiidae should be placed in the perciform suborder Xiphiioidei apart from the Scombroidei. Both followed Regan's (1909) and Gregory and Conrad's (1937) view that the Xiphiidae and Istiophoridae extend into basal Eocene time and that any common ancestry to each other and to the scombroids must have been prior to the Eocene and may have extended to the Cretaceous. These phylogenetic conclusions were partially based on the identifications by paleontologists who we now believe were in error. The following discussion is a critical review of billfish phylogeny and classification based primarily on fossil forms.

Woodward (1901) recognized that the Xiphiidae included all living billfish genera, as well as *Xiphiorhynchus*, *Acestrus*, and *Brachyrhynchus*. All the xiphiids were placed in the Division Scombriformes along with the scombrids, carangids, stromateids, and the extinct family Palaeorhynchidae. Woodward placed *Blochius* in the family Blochiidae in the division Blenniiformes. Regan (1909) placed the billfish in their own division, Xiphiiformes, within the perciform suborder Scombroidei. In this division he separated the istiophorids, xiphiids, and xiphiorhynchids into

their own families. In addition, Regan included the blochiids as a family within the Xiphiiformes.

The placement of the Paleorhynchidae with the xiphioids has been labeled as dubious (Gosline, 1968). According to Danil'chenko (1960), the paleorhynchids have about 45–60 vertebrae, jaws which are very elongate with the lower jaw sometimes longer than the upper, and ribs which completely surround the abdominal cavity. Thus, the paleorhynchids have about twice the vertebral number and have jaws and ribs unlike any living adult xiphioid. Until the paleorhynchids have been thoroughly studied, we prefer to put them in the Xiphiioidei *Incertae sedis*.

Woodward (1942) stated that *Blochius* does not exhibit the character of a xiphioid. Specimens of *Blochius* have a low vertebral number (24) and they lack (or have very reduced) pelvic fins, a condition similar to that found in living swordfish. However, blochiids are small (about 1 meter), have numerous dorsal and anal spines, have large scales, a round bill, and were living contemporaneously with the various species of *Xiphiorhynchus* and some istiophorids. Without question, the blochiids need additional study in order to determine their relationship and, until such research is accomplished, we prefer to put the Blochiidae in the Xiphiioidei *Incertae sedis*.

The relationship of the *Cylindracanthus*-group to the Xiphiioidei is also highly questionable. This group is only known by fossil rostra; no other skeletal remains have ever been positively identified. Encouraged by Woodward, Carter (1927) studied a *Cylindracanthus* rostrum from the Eocene of Nigeria. He showed that it was histologically similar to a fragment of a *Blochius* rostrum as well as to a dermal spine of an un-

TABLE 2. Rostral characters and chronological and geographical distributions of various billfish genera

Comparative Rostral Characters			
Taxon	Size and Shape of Cross-Section	Number of Longitudinal Nutrient Canals	Chronologic and Geographic Range
BLOCHIIDAE			
+ <i>Blochi</i>	small, round	unknown	Eocene, Europe
+ <i>Cylindracanthus</i> group	small, round	numerous	Cretaceous, Africa, Europe, North America to Oligocene, Europe
ISTIOPHORIDAE			
+ <i>Acestrus</i>	unknown	unknown	Eocene, Europe
<i>Istiophorus</i>	large, round	one pair	} Eocene, Europe, N America to recent, world-wide seas.
<i>Makaira</i>	large, round	one pair	
<i>Tetrapturus</i>	large, round	one pair	
+ <i>Brachyrhynchus</i>	large, round	one pair	Eocene to Pliocene, Europe
PALEORHYNCHIDAE			
+ <i>Enniskillenus</i>	unknown	unknown	Eocene, Europe
+ <i>Homorhynchus</i>	unknown	unknown	} Eocene to Oligocene, Europe
+ <i>Paleorhynchus</i>	unknown	unknown	
+ <i>Pseudotetrapturus</i>	(?) large, round	unknown	
XIPHIIDAE			
<i>Xiphias</i>	large, depressed	central and one pair	Oligocene, Europe to recent, world-wide seas.
+ undescribed genus	large, depressed	(?) central and one pair	Eocene, North America
XIPHIORHYNCHIDAE			
+ <i>Xiphiorhynchus</i>	large, round	central and two pair	Eocene, Europe, N. America, Africa
+ = extinct			

related living trunkfish (*Ostracion*). He concluded that the *Cylindracanthus* specimen was probably the bill of some extinct swordfish related to *Blochi*. This relationship has been accepted by most other ichthyologists and paleontologists (Berg, 1940; Casier, 1946, 1958; Darteville and Casier, 1943, 1949; Gregory, 1951; Leriche, 1942; and Romer, 1966). Recently Casier (1966) divided the *Cylindracanthus*-group into two parts and questionably put one part in the family Blochiidae of the Order Heteromi and the remainder in family Xiphiidae of the Order Scombromorphi (= ?Scombroidei). No explanation was given as to why he thought there was a relationship to the Order Heteromi (= Notacanthiformes). Woodward (1942) placed *Cylindracanthus* (= *Coelorhynchus*) in *Incertae sedis* and we agree with this decision. The transfer of the *Cylindracanthus*-group from the Xiphioidae proper removes all the pre-Eocene representatives.

On the basis of the above discussion, the seven

genera: *Acestrus*, *Brachyrhynchus*, *Istiophorus*, *Makaira*, *Tetrapturus*, *Xiphias*, and *Xiphiorhynchus* are all that remain as members of the Xiphioidae proper. Beginning with the living genera, we can reiterate that the Xiphiidae (*Xiphias*) is structurally very different from the Istiophoridae (*Istiophorus*, *Makaira*, *Tetrapturus*). *Xiphias* has a poor fossil record. Leriche (1910) identified a vertebra from the Oligocene of Belgium as *Xiphias rupelensis*, and we agree with his identification since the specimen is very similar to the penultimate vertebra of *X. gladius*. As far as we know, all other fossil records are erroneously based on istiophorids or members of the *Cylindracanthus*-group. Except for the rostrum, the skeleton of *X. gladius* is rather weak and fragile so that preservation is probably poor.

Not enough osteological information is known to distinguish between the rostra, skulls or vertebrae of the various recent or fossil istiophorids; therefore, exact identifications of fossil forms.

TABLE 3. Height to length ratios of the centra of certain billfish.

Species	3rd Vertebra	21st Vertebra
<i>Istiophorus platypterus</i> (Sailfish)	$\frac{30.5}{57.0} = .54$	$\frac{24.0}{66.5} = .37$
<i>Makaira indica</i> (Black marlin)	$\frac{52.5}{62.5} = .84$	$\frac{38.5}{83.5} = .46$
<i>Tetrapturus audax</i> (Striped marlin)	$\frac{30}{47} = .64$	$\frac{24}{61} = .39$
<i>Xiphias gladius</i> (Swordfish)	$\frac{43.0}{62.5} = .69$	$\frac{54}{72} = .75$
<i>Xiphiorhynchus kimblalocki</i>	Abdominal Vertebra $\frac{60.4}{70.0} = .86$	Caudal Vertebra $\frac{64.0}{92.5} = .69$

which are usually fragmentary, are to be questioned. Some of the fossil rostra may belong to *Xiphiorhynchus* and those identified as *Brachyrhynchus* are probably congeneric with *Istiophorus*, *Makaira*, or *Tetrapturus*. This latter observation was also noted by Woodward (1901). It seems, therefore, that *Brachyrhynchus* and the living istiophorids may form a continuum that dates from the Middle Eocene of Europe (Bruxellien).

Acestrus is only known from the early Eocene (London Clay-Ypresien) and the remains consist of posterior crania. Casier (1966) feels that these crania may belong to one of the other billfish genera, but not *Xiphiorhynchus*. *Acestrus*, like the living billfish, has pronounced muscle fossae on the dorsal surface of the posterior part of the cranium, whereas fossae seem to be lacking in *Xiphiorhynchus*. Casier (1966) also emphasizes that the cranium of *Acestrus* is very similar to that of the extinct scombroid, *Scombrinus*. All known cranial fragments of *Acestrus* are much smaller (they measure 50–60 mm in length) than the counterparts in living adult billfish and they are about one-half the size of the crania of *Xiphiorhynchus*. Even though the exact taxonomic placement of *Acestrus* is uncertain at best, we prefer to keep the genus in the Xiphioidae proper until more is known. It is possible that *Acestrus* is an immature billfish.

Xiphiorhynchus is intermediate in many respects to the Xiphiidae and Istiophoridae. Each frontal bone has ridges that radiate from a central point similar to the swordfish, whereas only the anterior

ridges are pronounced in the Istiophoridae. The ratio of the length of the posterior part of the cranium (anterior edge of the supraoccipital to the posterior edge of the exoccipital) to the length of the anterior part of the cranium (anterior edge of the mesethmoid to the posterior edge of the frontal) is about 0.35 for *Xiphiorhynchus priscus*, *T. audax*, *T. angustirostris*, *Istiophorus* sp. and *M. indica*. A similar ratio for *X. gladius* is 0.13, thus, the swordfish has a much smaller posterior region of the skull than other billfish.

The rostrum of *X. kimblalocki* appears to be broad at the base, similar to the swordfish, and it is round in the distal one-half, similar to the istiophorids (Table 1). Both the swordfish and *Xiphiorhynchus* have a central canal in their rostra, whereas the istiophorids have only lateral canals. However, *X. kimblalocki* lacks a central canal in the distal one-fourth of its rostrum. The abdominal vertebra of *X. kimblalocki* (Table 3) is similar in shape to the third vertebra of the black marlin (*M. indica*), yet the placement of the transverse process is similar to the third vertebra of the swordfish. In shape, the caudal vertebra of *X. kimblalocki* is similar to those of the swordfish.

It seems, therefore, that *Xiphiorhynchus* is intermediate between the Istiophoridae and the Xiphiidae and gives evidence that the two living billfish families diverged from a common ancestor prior to the Eocene. However, chronologically, *Xiphiorhynchus* is not able to be the common ancestor since it has never been found prior to the Eocene. There is no evidence that it is a

surviving parental stock. Very recently one of us (S.P.A.) collected a 75 cm section of a swordfish-like rostrum from the Yazoo Clay of the Eocene of Mississippi (Fierstine and Applegate, unpublished). This very depressed rostrum differs considerably from any rostrum known in Xiphiorhynchidae and Istiophoridae and demonstrates that a swordfish-like animal was living contemporaneously during the Eocene with the Xiphiorhynchidae and Istiophoridae. At this time we speculate that *Xiphiorhynchus* is an extinct offshoot from a yet unknown common ancestor and is closer to the Istiophoridae than to the Xiphiidae. Thus, even though based on different evidence, we must return to the conclusions of Regan (1909) and Gregory and Conrad (1937) that both the Xiphiidae and Istiophoridae extend into the basal Eocene and that any common ancestry to each other and to the scombroids must have been prior to the Eocene and may have extended to the Cretaceous.

Our proposed classification scheme for the billfish is as follows:

Class Osteichthyes

Order Perciformes

Suborder Xiphioidi

Family Istiophoridae: *Acestrus*, *Brachyrhynchus*, *Istiophorus*, *Makaira*, *Tetrapturus*.

Family Xiphiidae: *Xiphias* and undescribed genus.

Family Xiphiorhynchidae: *Xiphiorhynchus*.

Xiphioidi Incertae sedis.

Family Blochiidae: *Blochius*.

Family Paleorhynchidae: *Enniskillenius*, *Homorhynchus*, *Paleorhynchus*, *Pseudotetrapturus*.

Family unknown: *Cylindracanthus*-group.

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EVOLUTIONARY RELATIONSHIPS AND BIOGEOGRAPHY OF THE MACROTEIID LIZARDS (FAMILY TEIIDAE, SUBFAMILY TEINAE)

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ABSTRACT: The evolutionary relationships of nine genera of macroteiid lizards, *Ameiva*, *Cnemidophorus*, *Kentropyx*, *Dicrodon*, *Teius*, *Callopiastes*, *Crocodylurus*, *Tupinambis*, and *Dracaena* are discussed based on an analysis of 25 osteological character states. A phenetic scheme based on the average linkage technique and an evolutionary sequence diagram are presented. The result places the nine genera into two groups: A, *Ameiva*, *Cnemidophorus*, *Kentropyx*, *Teius*, and *Dicrodon*; B, *Callopiastes*, *Tupinambis*, *Crocodylurus*, and *Dracaena*. Group B is considered the most derived group of genera; *Dracaena* being the most derived genus.

An analysis of the fossil record of the macroteiids in association with present distributional patterns suggests that the ancestors of the macroteiids arose in North America and entered South America at the close of the Mesozoic Era. With the closure of the Panamanian Seaway in Early Pliocene, movement of *Ameiva* north and *Cnemidophorus* south, occurred. Subsequent geologic activity and contraction of the tropical climate, are responsible for the present distribution of the genera.

The lizard family Teiidae is composed of approximately 30 genera and 140 species. The group ranges throughout the New World from the northern United States, through Mexico and Central America to southern South America; several genera occur in the West Indies. The members of the family are primarily terrestrial, diurnal forms but some are semi-arboreal or semi-aquatic; many are semi-fossorial, being snake-like in appearance and habits. The family is comprised mostly of small lizards, the microteiids, but includes several genera of moderately large-sized lizards, the macroteiids; the largest of these, *Tupinambis* and *Dracaena*, reach a length of about a meter. Diets range from insectivorous to herbivorous; some are omnivorous and others strictly carnivorous (Presch, 1970). Food items cover a spectrum including aquatic snails, birds, eggs, and other lizards.

The purpose of this present study is to clarify the evolutionary relationships of one segment of the family Teiidae, namely the large teiid lizards *Ameiva*, *Cnemidophorus*, *Callopiastes*, *Dracaena*, *Kentropyx*, *Teius*, *Dicrodon*, *Tupinambis*, and *Crocodylurus*.

Few attempts have been made to place the various teiid genera into suprageneric groups. The accepted generic arrangement for the family Teiidae comes from the work of Boulenger (1884) in his systematic rearrangement of the Sauria. Prior to his work, the genera now referred to the Teiidae were placed in 27 separate families

by various authors (see Boulenger, 1884 for literature synonymy).

Boulenger (1885) split the family into four groups based on the condition of the scales on the nasal region. The macroteiids differ from the microteiids (terms first used by Ruibal, 1952) in having the anterior nasal plates not separated by frontonasal scales, limbs well-developed and, as the name implies, being medium to large in size. This division formed Group I in Boulenger's (1885) key and the division has been referred by recent workers (Uzzell, pers. comm.) as Group I of the Teiidae (*Ameiva*, *Callopiastes*, *Cnemidophorus*, *Crocodylurus*, *Dicrodon*, *Dracaena*, *Kentropyx*, *Teius*, and *Tupinambis*).

Group II, III, and IV of Boulenger's key were distinguished by: anterior nasal plates separated by one or two frontonasal plates, five fingers all clawed; nostril pierced between the nasal and the first labial; no ear opening; nasal plates widely separated by a frontonasal; ear exposed, inner finger, if distinct, clawless; respectively. These three groups contain the small teiid genera. This division has been referred to as the microteiids or Group II of the Teiidae: a group of small, secretive forms, several of which show a reduction in the limbs, climaxing in a limbless condition. This division includes: *Alopoglossus*, *Anadia*, *Anotosauria*, *Argalia*, *Arthrosauria*, *Bachia*, *Cercosaurus*,

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TABLE 1. Distribution of 21 character states in the Teiinae. See text for explanation of character state description.

	Postfrontal-Postorbital not(a) fused(b)	Quadrate process, Pterygoid not(a) expanded(b)	Pterygoid flange not(a) high(b)	Squamosal process present(a) absent(b)	Quadrate expanded yes(a) no(b)	Pterygoid teeth present(a) absent(b)	Premaxillary teeth simple(a) complex(b)	Clavicular shape expanded(a) rod(b)	Clavicular hook present(b) absent(a)	Intercavicle median proc. long(a) short(b)	Scapular fenestra present(a) absent(b)	No. postxiphisternal ribs 12(a) 11(b)	No. caudal vertebrae 60: more(a) less(b)	No. presacral vertebrae 26(a) 25(b)	Median crest on caudal vertebrae low(a) high(b)	Second ceratobranchial present(a) absent(b)	Anterior teeth on maxilla typical(a) complex(b)	Supra-angular window present(a) absent(b)	Ectopterygoid contribution to inferior orbital foramen large(a) small(b)	Shape frontal-parietal roof concave(a) other(b)	Condition fifth toe normal(a) other(b)
<u>Ameiva</u>	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a
<u>Cnemidophorus</u>	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	a	a
<u>Kentropyx</u>	b	b	b	a	a	a	a	a	a	a	a	a	a	a	a	a	a	a	b	b	a
<u>Dicrodon</u>	b	b	b	a	a	b	a	a	a	a	a	a	a	a	a	a	b	a	a	a	a
<u>Teius</u>	b	b	b	a	a	b	a	a	a	a	a	a	b	a	a	a	b	a	a	a	b
<u>Callopiestes</u>	a	a	a	b	a	a	a	b	b	a	b	b	a	b	b	a	a	a	a	b	a
<u>Tupinambis</u>	a	a	a	b	b	b	b	b	b	b	b	b	a	b	b	b	a	a	a	a	a
<u>Crocodylurus</u>	a	a	a	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a	a	a
<u>Dracaena</u>	b	a	a	b	b	b	b	b	b	b	b	b	b	b	b	b	b	b	a	a	a

Colobodactylus, *Colobosaurus*, *Echinosaurus*, *Ecleopopus*, *Euspondylus*, *Gymnophthalmus*, *Heterodactylus*, *Iphisa*, *Leposoma*, *Macropholidus*, *Microblepharus*, *Neusticurus*, *Opipeter*, *Pantodactylus*, *Pholidobolus*, *Placosoma*, *Ptychoglossus*, *Prionodactylus*, *Proctoporus*, *Teuchocercus*, and *Tretioscincus*.

Burt and Burt (1931) divided the family into the specialized genera and the lower teiids. The former include: genera with one or more specializations such as strongly compressed teeth (*Dicrodon*), the loss of digits (*Teius* and *Bachia*), the possession of weakened or vestigial limbs and serpentine form (*Ophiogonomon*, = *Bachia*, etc.), the loss of eyelids (*Gymnophthalmus*), the loss of ear openings (*Heterodactylus*), the separation of the prefrontals (*Calliscincopus* = *Tretioscincus*), the complete loss of the prefrontals (*Proctoporus*, *Pholidobolus*, etc.), loss of the frontonasal (*Ophiogonomon* = *Bachia*), enlargement of dorsal granules to scutes or a series of polygons (*Anadia*, *Euspondylus*, *Iphisa*, etc.), keeled ventral scales (*Kentropyx*, *Leposoma*), and very small size (*Microblepharus*, etc.). The remaining genera, the lower teiids, were divided into two subgroups: (1) genera with an essentially superiorly bi-

carinate tail; and (2) genera with a regular cyclotetragonal tail. The first group was comprised of *Dracaena*, *Neusticurus*, *Echinosaurus*, and *Crocodylurus*. The second group (*Callopiestes*, *Tupinambis*, and *Ameiva*) was considered the most primitive of the two and was indicated as the ancestral group from which the specialized teiids were derived.

Since Boulenger's work, there have been few papers on the systematic relationships of the large teiids. Cope (1900) stated that his description of the general characters, distributions and systematic arrangement of the genera were based on Boulenger (1885). Burt and Burt (1931) attempted to summarize and clarify the generic and specific characters of some of the genera. Vanzolini and Valencia (1965) maintained the division of the family into macroteiids and microteiids, on external morphology only, and discussed the possible relationships of the genus *Dracaena* in this framework.

A number of generic revisions have appeared in the last 55 years for members of Group I (macroteiids) and Group II (microteiids) (Uzzell, 1962, 1965, 1966; Vanzolini and Valencia, 1965; Vanzolini, 1961a, 1961b, 1961c, 1969; Ruibal,

TABLE 2. Evolutionary changes in certain characteristics of the skull and postcranial skeleton in the Tenu-

Characteristics	Primitive Condition	Derived Condition
Postfrontal-postorbital	separate (a)	fused (A)
Quadrate process of pterygoid	not expanded (b)	expanded (B)
Dorsal squamosal process	present (c)	absent (C)
Pterygoid teeth	present (d)	absent (D)
Premaxillary tooth types	conical (e)	biconodont, triconodont (E)
Clavicular shape	expanded (f)	rod-like (F)
Clavicular hooks	absent (g)	present (G)
Interclavicular median process	long (h)	short (H)
Scapular fenestra	present (i)	absent (I)
Divergent process series of caudal vertebrae or lack of caudal process	present (j)	absent (J)
Number of caudal vertebrae	more than 60 (k)	less than 60 (K)
Number of presacral vertebrae and post-xiphisternal ribs	26 vert., 12 post-xiphisternal ribs (l)	25 vert., 11 post-xiphisternal ribs (L)
Second ceratobranchial	present (m)	absent (M)
Tooth type	conical, biconodont triconodont (o)	molariform or medially expanded (O)
Supra-angular window	present (n)	absent (N)
Ectopterygoid contribution to inferior orbital foramen	much (p)	little (P)
Parietal-frontal shape	concave (q)	other (Q)
Fifth toe	normal (r)	reduction in skeletal elements (R)

1952; Duellman and Zweifel, 1962; Peters, 1964; Schmidt, 1957; Burt and Burt, 1931; Barbour, 1915; and Montanucci, 1973). These have provided a starting point for information on the evolutionary relationships of the genera involved.

METHODS

The study centers on a detailed analysis of the osteology of the nine genera of large teiid lizards. Both the cranial and postcranial skeleton was analyzed. The data on which the following discussion is based was taken from Presch (1970). The reader is referred to this work for details of methodology and detailed descriptions of the osteological elements mentioned below. The discussion is based on 21 osteological characters (Table 1) used by Presch (1970) to define and delimit the nine macroteiid genera.

DISCUSSION

Distribution of the character states in the nine macroteiid genera is summarized in table 1.

Table 2 summarizes the character states and the presumed direction of change or evolutionary trends. Information from these tables is useful in determining the major phenetic patterns. Similarity matrices are presented in table 3. Total similarity of shared character states (in roman type) and percentage of shared character states are presented. Table 4 presents a summary of the derived character states, the number and distribution among the nine genera.

Based on the percentage of total shared character states, regardless of whether the states are primitive or derived, the following groups are expressed. *Ameiva*, *Cnemidophorus*, *Dicrodon*, *Kentropyx*, and *Teius* share the greatest phenetic similarity (77 percent). The greatest similarity with the other genera is 48 percent. *Tupinambis*, *Callopistes*, *Crocodylus*, and *Dracaena* have a similarity of 66 percent intragenerically and only 30 percent with the former group of genera.

Data in table 2 suggest that the Teiinae (Presch, 1970) form two groups on the basis of the combination of shared character states: one group (Tribe Teiini) is comprised of *Ameiva*.

TABLE 3. Similarity matrices for Macroteiid genera. *Roman type*—number of shared character states; *Italics*—percent of shared character states.

		Genus							
		1	2	3	4	5	6	7	8
1	<i>Ameiva</i> and <i>Cnemidophorus</i>	—	20	18	16	6	3	9	13
2	<i>Kentropyx</i>	95	—	17	15	5	2	4	10
3	<i>Dicrodon</i>	86	81	—	19	7	6	6	8
4	<i>Teius</i>	76	72	90	—	5	6	6	6
5	<i>Tupinambis</i>	29	24	33	24	—	16	20	16
6	<i>Dracaena</i>	14	10	29	29	76	—	17	11
7	<i>Crocodylurus</i>	24	20	29	29	95	80	—	15
8	<i>Callopiestes</i>	43	48	38	29	76	52	71	—

Cnemidophorus, *Kentropyx*, *Teius*, and *Dicrodon*. The second group (Tribe Tupinambini) is composed of *Tupinambis*, *Callopiestes*, *Dracaena*, and *Crocodylurus*. The two groups have been defined formally as tribes (Presch, 1970).

Ameiva, *Cnemidophorus*, and *Kentropyx* share the greatest similarity (95 percent) with each other but only 72 percent and 81 percent with *Dicrodon* and *Teius*. The latter two genera share a 90 percent similarity. These results indicate *Ameiva*, *Cnemidophorus*, and *Kentropyx* are more closely related to each other than any is to *Dicrodon* or *Teius*.

In the Tupinambini, *Tupinambis*, *Crocodylurus*, and *Dracaena* share the greatest similarity (76–95 percent) with each other but only 52 and 76 percent with *Callopiestes*. These phenetic relationships are illustrated in an average linkage clustering method (Sokal and Sneath, 1963) phenogram (Fig. 1).

In an attempt to establish any evolutionary sequence for the macroteiid genera, weighting the osteological character states as either primitive or derived is necessary. There are several ways in which this has been done in the past (Kluge, 1967; Wake and Ozeti, 1969; Heyer, 1969; and Throckmorton, 1968).

The absence of a skeletal element is regarded as a more specialized condition than its presence. The direction of change in serial elements, increase or decrease, may be determined by outgroup comparison but with less confidence than when dealing with elements that are present or absent. Certain conditions are specialization but it is not always certain that such a specialization is not irreversible. Thus, in the evaluation of characters as primitive or derived, the greatest weight must be given to those characters which involve the complete loss of elements, less weight to those characters which involve some measure of judgment.

TABLE 4. Summary of derived character states. For clarity, only the derived states (capital letters) are shown in the body of the table.

	Characters															
	a/A	b/B	c/C	d/D	e/E	f/F	g/G	h/H	i/I	j/J	k/K	l/L	m/M	n/N	o/O	p/P
<i>Ameiva</i> and <i>Cnemidophorus</i>	A	B														
<i>Kentropyx</i>	A	B														Q
<i>Teius</i>	A	B		D					J	K					O	P
<i>Dicrodon</i>	A	B		D					J							P
<i>Tupinambis</i>			C	D	E	F	G		I			L	M			P
<i>Dracaena</i>	A		C	D	E	F	G	H	I		K	L	M	N	O	P
<i>Callopiestes</i>			C			F	G		I			L				P
<i>Crocodylurus</i>			C	D	E	F	G		I		K	L	M			P

pterygoid teeth, and the ventral orientation of the retroarticular process of the mandible (Presch. 1970). *Teius* is separated from *Dicrodon* by the reduction in the number of caudal vertebrae (*Dicrodon* with more than 60, *Teius* with less than 60), loss of the divergent process series in the caudal vertebral sequence and fusion and reduction in ankle bones.

Callopiastes differs from the other Group B members (hereafter referred to as the Tupinambini) in combining the presence of pterygoid teeth with biconodont and triconodont teeth on dentary and maxillary, premaxillary teeth simple in adults; second ceratobranchials present; clavicles without hooks; long interclavicular median process, reaching posteriorly to the level of the third sternal rib.

Tupinambis, *Crocodylurus*, and *Dracaena*, have lost the second ceratobranchials; loss of pterygoid teeth; a reduction in the length of the interclavicular median process to the level midway between the second and third sternal ribs, the loss of biconodont teeth on the dentary and maxillary, premaxillary teeth being biconodont in *Crocodylurus* and triconodont in *Tupinambis*. These three genera also share an increase in the expansion of the quadrate in a posteroanterior direction, beginning with *Crocodylurus* and *Tupinambis* and reaching its greatest expansion in *Dracaena*. The clavicles are simple in *Tupinambis*, with small hooks in *Crocodylurus*. *Dracaena* possesses large clavicular hooks and a further reduction in the interclavicle median process to the level of the second sternal rib.

Vanzolini and Valencia (1965) proposed a similar phylogenetic relationship based on 13 external scale characters. Gorman's (1970) interpretation based on chromosome morphology proposed a similar division: Group I with $2n = 50$ chromosomes; *Ameiva*, *Cnemidophorus*, *Kentropyx*, *Dicrodon*, and *Teius* with the same phylogenetic sequence as I have proposed. However, Group II with $2n = 34-38$ chromosomes, though containing the same genera as I propose, was arranged in a slightly different phylogenetic sequence.

BIOGEOGRAPHY OF THE MACROTEIIDS (SUBFAMILY TEIINAE)

The fossil history of the macroteiids dates back to the Late Cretaceous. Estes (1964) described several lizards of modern morphology from the Lance Formation of Wyoming which he referred to the Teiidae. These include *Chamops segnis*,

most similar to *Crocodylurus* and *Tupinambis*; *Meniscognathus ulymani* bearing resemblance to the modern *Kentropyx*. The affinities of two other forms, *Leptochamops denticulatus* and *Haptosphenus placodon*, to modern forms were unclear. Several vertebrae were also described and resemble those of the modern genera *Tupinambis* and *Crocodylurus*.

The genus *Chamops* is considered by Estes (1964) to be closely related to *Callopiastes*. I regard *Chamops* as a valid genus, but believe that it is more closely related to *Crocodylurus* than to *Callopiastes*. Estes (1964) described *Meniscognathus* and *Leptochamops* as being *Kentropyx*- or *Ameiva*-like. It is difficult to distinguish between *Ameiva*, *Cnemidophorus*, and *Kentropyx* based on the fragments of fossil maxillary and dentary pictured by Estes. However, I agree that it resembles these three modern genera more so than any other macroteiid genera.

Haptosphenus is referred to the family Teiidae, but shows a fused splenial, a characteristic of the family Xantusiidae. The teeth are pleurodont in the Xantusiidae but this does not agree with the teeth in *Haptosphenus*. Estes referred this genus to the Teiidae with the comment that further specimens may show a different familial relationship.

Estes (1961) described *Tupinambis teguixin* from the Late Oligocene of Colombia and a new species of *Dracaena* (*Dracaena colombiana*) from the Late Miocene of Colombia. I have studied his diagrams and agree with his allocation of the specimens to modern genera. There is no doubt that *Dracaena* and *Tupinambis* were present in the Oligocene of South America. Estes and Tihen (1964) reported specimens of the genus *Cnemidophorus* from the Valentine Formation, Miocene-Pliocene boundary of Nebraska. Etheridge (1964) described a fossil dentary from the Late Pleistocene of Barbuda, British West Indies, referring it to *Ameiva griswaldi*. *Ameiva chrysolaema* and *A. taeniura* were reported from the Late Pleistocene of the Dominican Republic by Etheridge (1965) and *A. thoracica* was reported from the Pleistocene of New Providence (Etheridge, 1965b).

Gilmore (1940) described two new genera and species of lizards, *Polyglyphanodon sternbergi* and *Paraglyphanodon utahensis*, from the Upper Cretaceous of South Dragon, Utah. After describing the osteology of *Polyglyphanodon sternbergi*, in detail, Gilmore (1942) erected a new family, the Polyglyphanodontidae, recognizing only that it was not related to either the Iguanidae

or Agamidae, and placed it in the Ascalabota division of the Sauria. In 1943 Gilmore described a new species, *Paraglyphanodon gazini* and placed the genus in the family Polyglyphanodontidae.

Hoffstetter (1955) recognized *Polyglyphanodon sternbergi* as belonging to the family Teiidae. The genus *Paraglyphanodon* is currently under study but it probably belongs to the family Teiidae (Estes, pers. comm.).

Estes (1969) described a new teiid genus and species, *Peneteius aquilonius*, from the Late Cretaceous Hell Creek Formation, Montana. He believed it occupied a position midway between *Polyglyphanodon* and the modern genera *Teius* and *Dicrodon*.

The presence of *Tupinambis*, *Teius*, *Ameiva*, and *Cnemidophorus* in the Oligocene and *Dracopis* in the Miocene indicates an early origin for the macroteiid genera. It seems likely that the modernization of this group of genera took place not later than the Oligocene and quite probably much earlier. The presence in the late Cretaceous of *Meniscognathus*, a form that Estes considers to be *Ameiva-Kentropyx*-like indicates that the ancestor for the Teiini were present by the middle or late Mesozoic.

The distribution of the macroteiid genera is restricted to South America with the exception of *Ameiva* and *Cnemidophorus*. It seems likely that the ancestor of the modern macroteiids reached South America sometime late in the Cretaceous or early Paleocene across the Panamanian land-bridge (Savage, 1966) and underwent independent evolution during the period of isolation in South America from the late Paleocene to the early Pliocene.

The ancestors of modern *Ameiva-Cnemidophorus* appears to have evolved in isolation in two areas north and south of the Panamanian portal throughout middle Cenozoic (Eocene-Miocene). Both diverged to a level of generic differentiation and some northern forms seem to have reached South America and several South American forms. Middle America, after the land connection was re-established in the Pliocene (Savage, 1966).

In summary the family Teiidae is a strictly New World family, originating in the tropical to warm temperate areas of North America. The modern macroteiids are restricted to South America and probably arose in South America in the early Tertiary. *Cnemidophorus* and *Ameiva* appear to have been derived from a common ancestor, and evolved in North America and South America, in isolation through much of the Cenozoic.

The history of the macroteiid genera seems to parallel the development of the marsupials, caviomorph rodents, and primates in South America (Savage, 1973).

The geological history of the South American land mass has played an important role in the present distribution of the macroteiid genera. There is some discussion as to the exact time of separation of the North American land mass from South America. Savage (1972) reviewed the evidence of both Simpson (1940) and Hershkovitz (1969), using mammalian distributions, and reached the same conclusion as he did in 1966 based on the analysis of the herpetofauna of Central America. The landbridge between Central America and South America was submerged from the late Paleocene to the early Pliocene. However, as pointed out above, the ancestors of the macroteiids were present by the close of the Mesozoic and probably crossed into South America prior to the formation of the Panamanian Seaway. Those events which have shaped the present distribution of the macroteiids must then be restricted to the events which occurred from the beginning of the Cenozoic to the present time in South America.

There are no complete studies on the geological history of South America, but there are several papers which review the major events that took place during the Cenozoic period (Kummel, 1961; Harrington, 1962; Lloyd, 1963). Likewise, the climatic changes during this time are generally known and summarized by Axelrod (1960).

Though there are a great number of events which shaped the distribution of the macroteiids in South America, the most important geological occurrences are: 1) the uplift and formation of the Andean Mountain Range, beginning in the Paleocene, and ending in the Pleistocene. 2) the extensive flooding of vast areas of parts of the Amazonian, Parnaiba and San Francisco Basins and the extreme stability of the Guiana, Central Brazilian and Coastal Brazilian Shields (Harrington, 1962).

The uplift and formation of the Andean mountain chain began in the Paleocene and lasted until the late Pleistocene (Kummel, 1961). The greatest uplift occurred during the late Pliocene or early Pleistocene (Haffer, 1967; Harrington, 1962). The sea advanced several times during the Cenozoic into the Amazonian, San Francisco Basins, and the southern Patagonian Basin, as well as areas in what is today northern Colombia and Venezuela.

During this period of geological compression, folding and uplift, two areas apparently were little affected; the Guiana and greater Brazilian Shields. Harrington (1962), pointed out the stability of these shields, dating back to early Precambrian. These areas were not subject to major geological activity, nor were they ever flooded. They were relatively stable, geologically and probably places of relative environmental stability.

The climate during the Cenozoic of South America has been summarized by Axelrod (1960) by inference from known Cenozoic fossil floras. The tropical and subtropical flora extended south to a latitude of 45° – 50° . In response to lower temperature during the Eocene, the tropical climatic belt was reduced as indicated by the reduction of the Neotropical Geoflora (Axelrod, 1960). During the middle to late Tertiary, dry climates developed along the east and west coast of South America, gradually confining the tropical flora to its present region (Axelrod, 1960).

The fossil history of the macroteiids as outlined above, along with the extent of the tropical floras, indicates that this group has always been confined to areas of tropical to warm-temperate climate. This association with climate is represented today with the exception of some of the northern species of *Cnemidophorus*.

Callopiastes and *Dicrondon* are dry-adapted groups which probably became restricted to the west coast of South America in the Late Pliocene when the main uplift of the Andes took place.

Teius is found in an area of South America which has remained relatively stable and dry since the Late Oligocene. Its arrival in southern South America probably dates to the early Cenozoic and has remained there undergoing little change.

Ameiva and *Kentropyx* today occupy a vast range in South America and are composed of about 32 and 7 species, respectively. It seems most probable that, during the entire Cenozoic, these two groups were repeatedly broken into fragmentary populations by the many geological events which occurred, undergoing speciation and expanding their ranges as conditions permitted.

Throughout the Cenozoic, northwestern Colombia was repeatedly flooded, causing an extremely unstable environment, hostile to the survival of the macroteiids. With the closure of the last portion of the Panamanian Portal, in the early Pliocene, faunal interchange between North and South America became possible. *Cnemidophorus*, which evolved in North America, was able to move into South America, while South American

forms of *Ameiva* were able to move north into Central America and Mexico. *Cnemidophorus* maintained its distribution in North America and was able to adapt to the change in climatic conditions (Axelrod, 1948) which occurred throughout the Cenozoic.

Tupinambis and *Dracaena* are both humid-tropical forms. *Dracaena* is particularly abundant in tidal and marshy sections of the Amazon Valley and in the drier ground on the fringes of the swamps in southern Brazil. *Tupinambis* occurs over much of the forested areas of tropical South America. Fields (1957, 1959) has described the northern section of Colombia during the Miocene, from which *Dracaena* and *Tupinambis* are known, as being a wet-tropical climate. Fields describes part of this region today as having a semi-arid climate, a condition unfavorable to *Tupinambis* and *Dracaena*. *Crocodylus* is also a wet-tropical form, found in association with small, slow-moving rivers (Goeldi, 1902). It appears that these three genera occupied the wet-tropical areas of South America in the early Tertiary, but as the climatic conditions changed in the middle to late Tertiary these forms followed the contraction of the tropical flora and climate, their habitat being restricted both by the Andean uplift and, to a great extent, by the increasing aridity.

MATERIAL EXAMINED

The following species of teiid lizards were studied from radiographs, as dry skeletons, or both. Each species is followed by the number of specimens examined.

Teiinae:

Ameiva: *ameiva* (12), *auberi* (2), *bifrontata* (9), *bridgei* (1), *chrysolasma* (5), *dorsalis* (2), *erythrocephalus* (2), *exsul* (2), *festiva* (22), *fuscata* (2), *griswoldi* (2), *leptophrys* (4), *lineolata* (4), *maynardi* (2), *pleii* (2), *pluvianotata* (2), *polops* (2), *quadri-lineata* (7), *septemilineata* (2), *taeniura* (4), *undulata* (12), *wetmorei* (4).

Callopiastes: *flavipunctatus* (9), *maculatus* (13).

Cnemidophorus: *angusticeps* (3), *burti* (2), *calidipes* (2), *ceralbensis* (2), *communis* (1), *costatus* (13), *cozumela* (2), *deppi* (10), *exsanguis* (3), *gularis* (2), *guttatus* (3), *hyperythrus* (5), *inornatus* (2), *labialis* (1), *lacertoides* (1), *lemniscatus* (31), *lineatissimus* (2), *maximus* (1), *motaguae* (4), *murinus* (10), *neomexicanus* (3), *ocellifer* (2), *sacki* (1), *septemvittatus* (5), *sexlineatus* (2), *sonorae* (3), *tigris* (13), *uniparens* (2), *velox* (2), *vanzoi* (6).

Crocodylus: *lacertinus* (8).

Dicrodon: *guttulatum* (20), *heterolepis* (3), *holmbergi* (3).
Dracaena: *guianensis* (12), *paraguayensis* (4).
Kentropyx: *altamazonicus* (1), *calcaratus* (21),
pelviceps (7), *striatus* (15), *viridistriga* (2), *williamsi* (1).
Teius: *teyou* (11).
Tupinambis: *rufescens* (52), *teguixin* (55).

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PARASITIC BOPYRID ISOPODS OF THE AMPHI-AMERICAN GENUS *STEGOPHRYXUS* THOMPSON WITH THE DESCRIPTION OF A NEW SPECIES FROM CALIFORNIA

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ABSTRACT: *Stegophryxus hyptius*, heretofore known only as a parasite of *Pagurus longicarpus* in New England, is recorded infesting *P. longicarpus* in Georgia, *P. annulipes* in North Carolina and Georgia, and *P. bonairensis* and *P. miamensis* in southern Florida. The only known specimens of *Stegophryxus thompsoni*, the types, from an unknown host in Chile are redescribed. A new species from California and Baja California, *S. hyphalus*, is described as a parasite of *Parapagurodes laurentae* and *P. makarovi*. These three species, the only members of the genus, are illustrated in detail and their distribution discussed.

Examination of shallow-water hermit crabs collected along the Atlantic coast from Florida to North Carolina has turned up several specimens of the athelgine bopyrid parasite *Stegophryxus hyptius* Thompson, previously known only from New England, thereby providing several new host records and a considerable extension of range for this species. Reexamination of the types of *S. thompsoni* Nierstrasz and Brender à Brandis from Chile, which had not been adequately described, became possible. Numerous parasites of hermit crabs taken off the coast of California and Baja California proved to belong to a new species. With these three species of *Stegophryxus* described, it became possible to review the genus in detail.

The material examined was in or has been donated to the following museums: Allan Hancock Foundation, University of Southern California (AHF); Rijksmuseum van Natuurlijke Historie, Leiden (RMNHL); Rosenstiel School of Marine and Atmospheric Science, University of Miami (UMML); United States National Museum of Natural History, Smithsonian Institution (USNM); and Universitetets Zoologiske Museum, Copenhagen (ZMC).

Stegophryxus Thompson 1902

Type-species, by original designation, *Stegophryxus hyptius* Thompson.

Stegophryxus hyptius Thompson 1902 Figures 1-3

Stegophryxus hyptius Thompson, 1902, pp. 53-56, pls. 9, 10.—Richardson, 1904, pp. 59-60; 1905, pp. 532-535, figs. 578, 579.—Rathbun, 1905, p. 48.—

Sumner *et al.*, 1913a, p. 136; 1913b, p. 661.
Kunkel, 1918, p. 236.—Reinhard *et al.*, 1947, pp. 70-72.—Reinhard, 1949, pp. 17-31; 1956, p. 101.
Reinhard and Buckeridge, 1950, p. 131.—Caullery, 1950, p. 97; 1952, p. 76.—Reverberi, 1952, p. 292.—von Brand, 1952, pp. 256, 271, tab. 41; 1966, p. 222, tab. 38.—Floorkin, 1960, p. 405.—Noble *et al.*, 1964, pp. 392, 393, figs. XVI-5A, 5B, 5C.—Smith, 1964, p. 105.—Kaestner, 1970, p. 463.
Bourdon, 1968, p. 133.—Schultz, 1969, pp. 321-322, fig. 513.—Markham, 1972, p. 73.
Stegophryxus hyptius.—Miner, 1950, pp. 450, 453, pl. 145.
Stegophryxus hyptius.—Nierstrasz and Brender à Brandis, 1931, pp. 197-198.
Stegophryxus.—Baffoni, 1953, p. 447.—Reinhard, 1956, p. 93.—Kaestner, 1967, p. 1161; 1970, pp. 425, 463.

Material examined.—Infesting *Pagurus bonairensis* Schmitt, Bear Cut, Virginia Key, Miami, Florida, 9 February 1958, A. J. Provenzano, coll., 1♀, 1♂, USNM 101762. In *Thalassia* bed, shallow water, NW side Virginia Key, Miami, Florida, 25 March 1969, J. C. Markham, coll., 1♀, 1♂ (reference ♀), USNM. Same locality, 8 November 1972, E. B. Hatfield, coll., 1♀, 1♂, AHF. Same locality, 12 February 1973, E. B. Hatfield, coll., 1♀ (reference ♀), 1♂, USNM. Shallow subtidal, off W. Arsenicker Key, Card Sound, Florida, 25 October 1972, E. B. Hatfield, coll., 1♀, 1♂, UMML 32.4538.

Infesting *Pagurus miamensis* Provenzano. In *Thalassia* bed, shallow water, NW side Virginia Key, Miami, Florida, 28 June 1972, E. B. Hatfield, coll., P. A. McLaughlin, identification of host, 1♀, 1♂, UMML 32.4539.

Infesting *Pagurus longicarpus* Say. Tidepool, Sapelo

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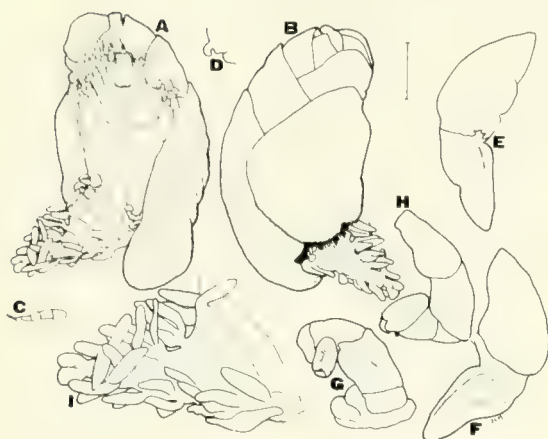


Figure 1. *Stegophryxus hyptius* Thompson, reference female. A. Dorsal view. B. Ventral view. C. Left antenna 2. D. Right posterior ventral border of head. E. Right oostegite 1, interior. F. Same, exterior. G. Right pereopod 1. H. Left pereopod 7. I. Pleon, dorsal view. Scale indicates 1.0mm for A, B, 0.5mm for D-F, I, 0.2mm for C, G, H.

Beach, Georgia, August 1969. R. W. Heard, coll., one immature ♀, 1 ♂, USNM. Woods Hole, Massachusetts, date and coll. unknown, M. J. Rathbun, identification of host, 1 ♀, 1 ♂, USNM 54777.

Infesting *Pagurus annulipes* Stimpson, all hosts identified by P. A. McLaughlin. Morehead Channel, North Carolina, 3 March 1967, R. W. Heard, coll., 3 ♀, 3 ♂, four cryptoniscan larvae, ZMC. Same locality, 25 June 1970, R. W. Heard, coll., 4 ♀, 4 ♂,

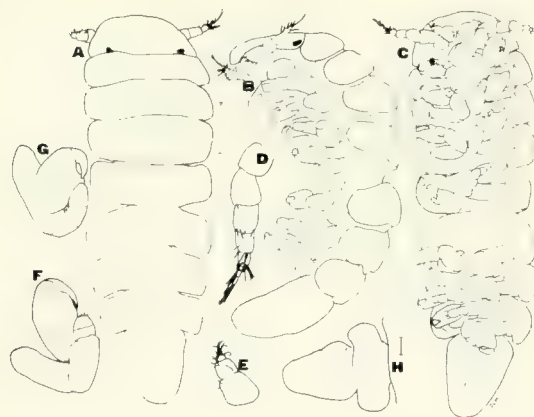


Figure 2. *Stegophryxus hyptius* Thompson, A-G, reference male. H. Second male. A. Dorsal view. B. Lateral view. C. Ventral view. D. Right antenna 2. E. Left antenna 1. F. Right pereopod 1. G. Left pereopod 7. H. Pleon and last pereomere, dorsal view. Scale at B, indicates 0.2mm for A-C, 0.1mm for D-G; scale at H, indicates 0.1 mm for H.

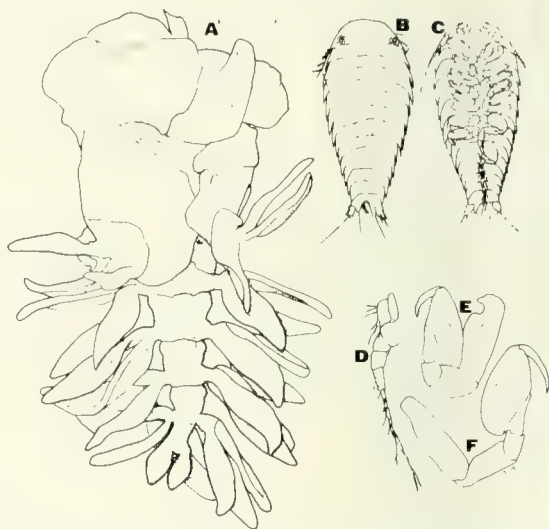


Figure 3. *Stegophryxus hyptius* Thompson. A. Immature female, ventral view. B-F, cryptoniscan larva. B. Dorsal view. C. Ventral view. D. Left antennae. E. Left pereopod 1. F. Left pereopod 7. Scale indicates 1.0mm for A, 0.1mm for B, C, 0.05mm for D-F.

two cryptoniscan larvae, RMNHL. Lacking collection data (probably North Carolina), 1 ♀, UMML 32.4540. Beaufort, North Carolina, 1969 or 1970, C. Kellogg, coll., 1 ♀, 1 ♂, AHF. Same, 1 ♀, 1 ♂, both damaged, UMML 32.4541. Bulkhead Channel, Beaufort Harbor, North Carolina, 22 June 1970, C. Kellogg, coll., 1 ♀, 1 ♂, AHF. Same, 1 ♀, 1 ♂, UMML 32.4542. Beaufort Harbor, North Carolina, 1969 or 1970, C. Kellogg, coll., 1 damaged ♀, AHF.

Remarks.—Thompson (1902) presented a detailed description and excellent drawings of both sexes, an immature female and a cryptoniscan larva of *Stegophryxus hyptius*. Richardson (1905) reproduced Thompson's descriptions and drawings of the adults. There is thus no need to re-describe this species in detail, and a diagnosis should suffice. For comparison, I have presented drawings of both sexes collected in Florida (Figs. 1, 2), an immature female from Georgia (Fig. 3A) and more detailed drawings of a cryptoniscan from North Carolina (Figs. 3B-F).

The characters which distinguish the females of *S. hyptius* (Fig. 1) are a head twice its width, a first oostegite which is bluntly pointed, a highly asymmetrical brood pouch which extends far back on the right side, a pleon which is less than half the total body length and bears very narrow lateral plates and pleopodal rami and enlarged prominent uropods. Males of *S. hyptius* (Fig. 2) are distinctive in having conspicuous eyes, the head clearly

separated from the pereon, and the pleon markedly narrower than the last pereomere, roughly triangular and ending in a rounded point. The immature female of *S. hyptius* can be distinguished by its lack of coxal plates, its elongate pleomeres and very prominent uropods.

Two of the host *Pagurus annulipes*, in addition to bearing mature pairs of *Stegophryxus hyptius* on the abdomen, also bore cryptoniscan larvae on the thorax. On one *P. annulipes* there were two cryptoniscans, one attached to the carapace, the other to a pereopod; on the other *P. annulipes*, three cryptoniscans were clinging to the carapace and a fourth was inside the branchial chamber. These larvae, one of which is pictured (Figs. 3B-F), agree in all respects with those which Thompson (1902) described, even though he found them with the male in the brood chamber of the female *Stegophryxus* rather than on the host's body. I have sent some of these larvae to Jarl-Ove Strömberg of the University of Lund, who plans to examine them with a scanning electron microscope.

One pair of *Stegophryxus hyptius* from *Pagurus bonairensis* was examined while still alive. The female was clinging so tightly to its host's pleopods that one pleopod was torn off in removing the parasite. Its only movement was a constant beating of the anterior oostegites to aerate the larvae filling the closed brood pouch. The male, rather than being in the female's brood pouch, as is typical, was crawling all over its body. The color of the female was transparent to whitish except that dorsally the gut was red-orange and the ovaries yellowish with developing eggs, and there were a few chalky white chromatophores scattered along the sides. The male was transparent except for black eyespots, a brownish gut and a network of interconnecting white lines in all pereomeres and the posterior third of the pleon. A second pair was examined freshly preserved. The female had a uniform glossy white background with brick-red eyes, a pale yellow central dorsal region on the pereon and a few chalky white chromatophores scattered near the edges of the pereon; developing embryos visible through the oostegites bore rows of punctate red chromatophores. The accompanying male was also glossy white with black eyespots, an orange gut and scattered black and white chromatophores.

Previous records of *S. hyptius* are only from Rhode Island and Woods Hole, Massachusetts. At the latter locality it is so common that Reinhard (1949) used it in a classical study to demonstrate

sex determination in the Bopyridae, and Reinhard *et al.*, (1947) made important discoveries about the effects it had on its host, which was always *Pagurus longicarpus*. The new records thus add a considerable extension of range, down to southern Florida, and several new host records, all species of *Pagurus*.

Of the parasites examined, 17 were still with their hosts. Five of these hosts were males, 12 females, the females being hosts significantly more often.

Stegophryxus thompsoni Nierstrasz

and Brender à Brandis 1931

Figures 4-5

Stegophryxus thompsoni Nierstrasz and Brender à Brandis, 1931, pp. 196-198, figs. 87-89

Material examined.—From unknown hermit crab Valparaíso, Chile, exact locality and date unknown. Th. Mortensen Pacific Expedition, coll. Holotype allotype ♂, both damaged, ZMC.

Redescription of holotypic female (Fig. 4).—Body length 8.0mm, maximal body width 3.7mm, head length 1.6mm, pleon length 3.8mm, distortion of body axis 50 degrees. Body badly damaged, so outline uncertain (Fig. 4A).

Head twice as long as wide. Segmentation of antenna 1 uncertain, antenna 2 (Fig. 4B) of five



Figure 4. *Stegophryxus thompsoni* Nierstrasz and Brender à Brandis, holotype female. A. Dorsal view. B. Right antenna 2. C. Right maxilliped. D. Right posterior ventral border of head. E. Right oostegite 1, interior. F. Same, exterior. G. Left pereopod 2. H. Right pereopod 6. I. Pleon, ventral view. Scale indicates 1.0mm for A, C, E, F, I. 0.4mm for B. 0.25mm for D, 0.5mm for G, H.

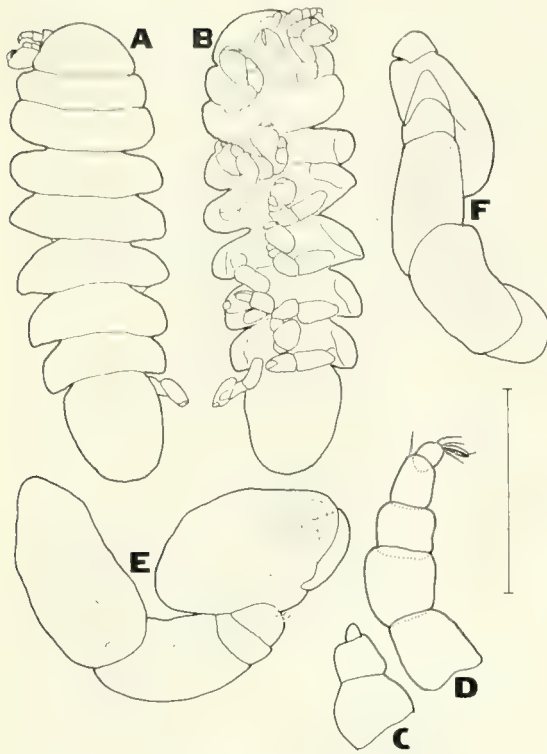


Figure 5. *Stegophryxus thompsoni* Nierstrasz and Brender à Brandis, allotype male. A. Dorsal view. B. Ventral view. C. Left antenna 1. D. Left antenna 2. E. Right pereopod 1. F. Right pereopod 7. Scale indicates 1.0mm for A, B. 0.2mm for C-F.

segments. No eyes. Maxilliped (Fig. 4C) with very irregular outline. Posterior ventral border of head (Fig. 4D) with long pointed lateral projection, irregular blunt process medial to it.

Pereon surrounding head, first two pereomeres obliterated centrally, first five surrounding head, sixth longest. First oostegites (Figs. 4E, F) rounded anteriorly, with dentate internal ridge, sharply angled falcate posterolateral point. Most of other oostegites damaged or missing, so size, shape and position unknown. First five pereopods with prominent coxal plates, sharply reflexed, reduced in size (Fig. 4G); last two pereopods lacking coxal plates, more or less straight, larger (Fig. 4H). Last two pereomeres (Fig. 4I) with medial ventral tubercles near anterior margins.

Pleon nearly as long as pereon, gradually tapering posteriorly, of six pleomeres. Lateral plates and pleopodal rami (Fig. 4I) all about the same size, ovate in outline; evidently pleopods and lateral plates lost from fourth and fifth pleomeres by damage. Uropods uniramous, oval, each nearly as large as whole last pleomere, extending far posteriorly from that pleomere. Tiny posterior point between uropods.

Redescription of allotypic male (Fig. 5).—Body length 2.3mm, maximal body width 0.8mm, head length 0.3mm, pleon length 0.6mm. Sides of body nearly parallel, all segments clearly separated (Figs. 5A, B).

Head semicircular, narrower than pereon. No eyes. Antennae (Figs. 5C, D) of three and five segments, respectively.

Pereon broadest, but only slightly so, across fourth pereomere. All pereomeres separated by slight anterolateral indentations. Pereopods (Figs. 5E, F) gradually smaller posteriorly.

Pleon nearly as broad as last pereomere, barely longer than wide, broadly oval in outline, greatest width about $\frac{1}{3}$ of distance back from anterior edge. No indication of segmentation.

The male has broken into two pieces between the third and fourth pereomeres, and one side of the pleon is damaged, so the drawings presented are partial reconstructions.

Stegophryxus hyphalus, new species

Figures 6-8

?*Stegophryxus* sp.—Menzies and Miller, 1954, pp. 141, 153.

Stegophryxus n. sp.—McLaughlin and Haig, 1973, pp. 119, 134-135.

Material examined.—Infesting *Parapagurodes laurentae* McLaughlin and Haig (part of type series) collected by Allan Hancock Foundation Velero III among Santa Barbara Islands, California, and near Abrejos Pt., Baja California. Sta. 914-39, 32°47'N, 118°22'W, 143-319m, 19 February 1939, 1♀, 1♂, AHF; Sta. 981-39, 33°35'-35°08'N, 119°01'W, 139-159m, 29 May 1939, 1♀, 1♂, AHF; Sta. 1012-39, 32°46'N, 118°25'W, 100-126m, 9 November 1939, one immature ♀, AHF; Sta. 1028-39, 33°18'N, 118°16'W, 152-229m, 10 December 1939, 1♀, 1♂, ZMC; Sta. 1239-41, 33°01'N, 118°33'W, 95-112m, 22 February 1941, 1♀, AHF; Sta. 1429-41, 33°17'N, 118°16'W, 159-174m, 25 October 1941, 5♀, 1♂, AHF; Sta. 1710-49, 26°17'N, 113°41'W, 99m, 7 March 1949, one immature ♀, USNM; Sta. 1937-50, 34°02'N, 119°27'W, 69-79m, 24 March 1950, one immature ♀, ZMC.

Infesting *Parapagurodes makarovi* McLaughlin and Haig (part of type series) collected by U.S. Bureau of Fisheries Steamer Albatross. Sta. 2946, in Santa Barbara Islands, California. 33°58'N, 119°31'W, 274m, 7 February 1889, 1♀, USNM. Sta. 3184, off Carmel, California. 36°27'N, 122°00'W, 141m, 3 April 1890, 1♀, 1♂, USNM. Collected by Velero III among Santa Barbara Islands, California, and near San Benito Islands, Baja California. Sta. 911-39, 39°00'N, 118°33'W, 110-155m, 18 February 1939, 1♀, 1♂, AHF; Sta. 981-39, 33°35'N, 119°01'W, 139-159m, 29 May 1939, 7♀ (including one immature), 3♂, AHF; Sta. 983-39, 33°44'N, 119°10'W,

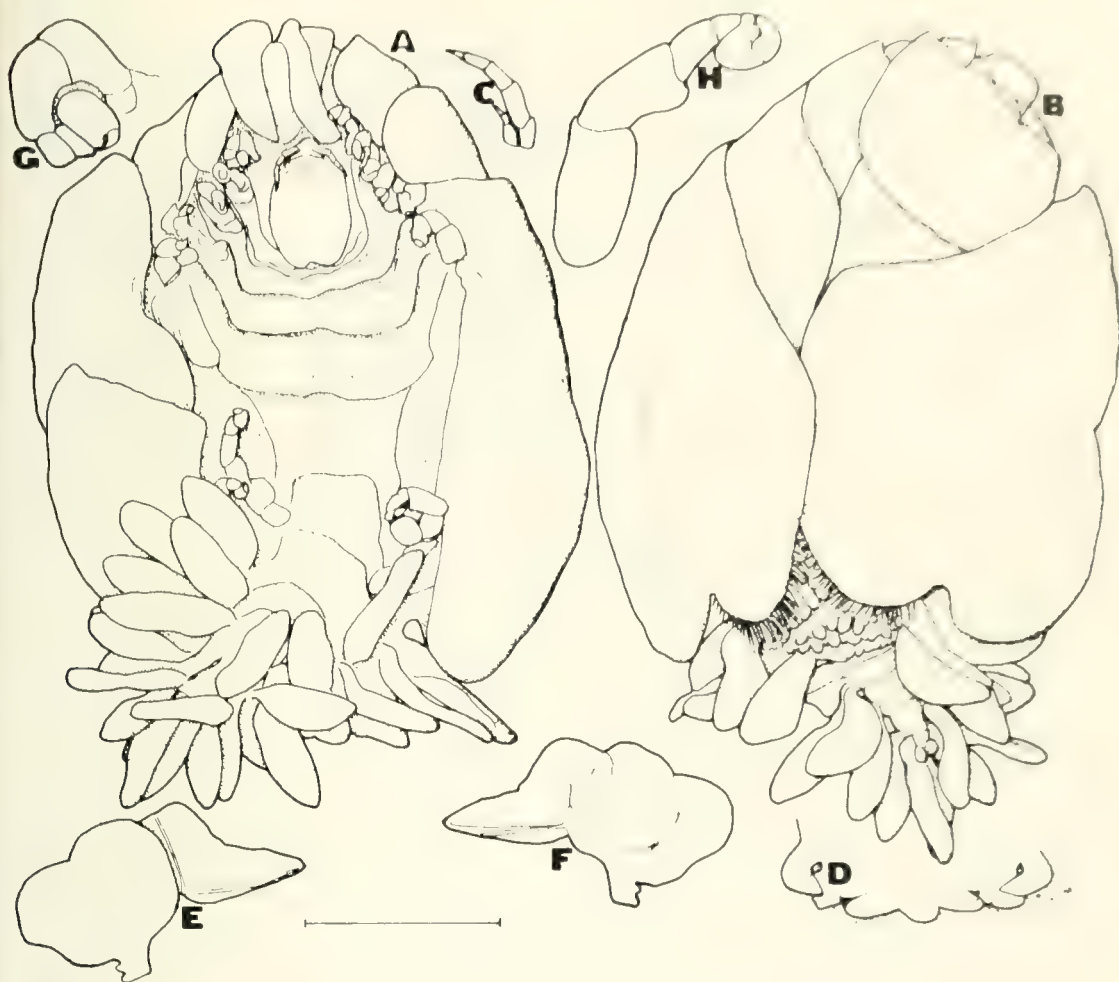


Figure 6. *Stegophryxus hyphalus*, new species, holotype female. A. Dorsal view. B. Ventral view. C. Left antennae. D. Posterior ventral border of head. E. Right oostegite 1, exterior. F. Same, interior. G. Left pereopod 1. H. Left pereopod 6. Scale indicates 2.0mm for A, B. E, F, 1.0mm for D, 0.5mm for C, G, H.

128m, 29 May 1939, 1♀, AHF; Sta. 1018-39, 33° 01'N, 118°32'W, 110-247m, 23 November 1939, one immature ♀, RMNHL; Sta. 1020-39, 33°03'N, 118° 40'W, 247-274m, 24 November 1939, 2♀, 1♂, AHF; Sta. 1026-39, 33°00'N, 118°38'W, 216-384m, 9 December 1939, holotype ♀, AHF 3928, allotype ♂, AHF 3928a, two other ♀, one other ♂, AHF; Sta. 1119-40, 28°13'N, 115°34'W, 159-174m, 19 February 1940, 1♀, UMML 32.4543; Sta. 1173-40, 33° 17'N, 118°14'W, 197-201m, 20 August 1940, 1♀, AHF; Sta. 1393-41, 33°47'N, 119°59'W, 196-229m, 26 August 1941, 1♀, 1♂, RMNHL. Collected by Velero IV near Santa Barbara Island, Sta. 2062-51, 33°33'N-34°33'N, 119°04'W, 256-296m, 18 October 1951, 1♀, 1♂, UMML 32.4544.

Description of holotypic female (Fig. 6).—Body

length 6.1mm, maximal body width 3.2mm, head length 1.2mm, pleon length 2.3mm, distortion of body axis 42 degrees. Body nearly oval in outline (Figs 6A, B).

Head roughly cordate in shape, about 1.5 times as long as broad. Antennae 1 and 2 (Fig. 6C) of 3 and 5 segments, respectively; each segment smaller than that proximal to it. No eyes. Posterior ventral border of head (Fig. 6D) with raised central portion consisting of a blunt medial point and two laterally directed narrow rounded points; each side bearing a long tapering point laterally with irregularly shaped blunt projection medial to it.

Pereon longer than broad. First five pereomeres concave anteriorly, more or less concentrically surrounding head; first two pereomeres incomplete in

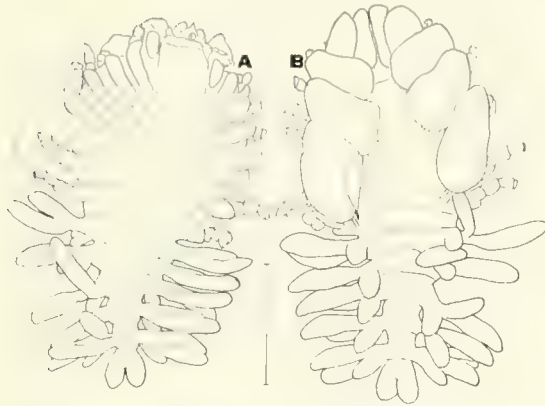


Figure 7. *Stegophryxus hyphalus*, new species, immature female. A. Dorsal view. B. Ventral view. 1.0mm indicated.

center: last two pereomeres concave posteriorly, narrower than others; sixth pereomere by far the longest. First oostegites (Figs. 6E, F) rounded anteriorly, without conspicuous internal ridge in circular middle region, produced into broadly falcate posterolateral point; first two pairs of oostegites arching over head; fifth oostegites by far the largest, covering half of ventral surface, both produced into posterolateral pockets of equal length, posterolateral borders lined with several long setae. Pereopods of first five pairs (Fig. 6G) surrounding head, sharply reflexed; last two pereopods (Fig. 6H) far posterior, longer and straighter than others.

Pleon about $\frac{3}{5}$ as long as pereon, of six pleomeres. Numerous tubercles on ventral surface of first two pleomeres. Sides of pleomeres 1-5 produced into foliaceous lanceolate lateral plates identical to branches of biramous pleopods. Final pleomere bearing small bulbous uniramous uropods.

Variations: Some of the other females examined show a few slight variations from the type. In several cases, the uropods are somewhat longer; in others, the tubercles on the first two pleomeres are either longer and flatter or absent. Ten of the 33 females examined are immature to varying degrees, so remarks on their development are possible. At first, the body is nearly symmetrical, the small oostegites of equal size in each pair, gradually larger from the first to the fifth; the pleon, which is as long as the pereon and not abruptly narrower than it, extends straight back. In the earliest postlarval stages, only the exopodites of the pleopods are developed, the endopodites being small flaps and the lateral plates suggested by tiny bumps. As development progresses (Fig. 7), the branches of the pleopods become equal, while the corresponding lateral plates are still smaller. Other conspicuous differences of the immature females from adult ones are large coxal plates at the bases of all pereopods and much larger uropods.

Description of allotypic male (Figs. 8A-E).—Body length 2.6mm, maximal width 0.6mm, pleon length 0.7mm. Sides of pereon nearly parallel, head and pleon abruptly narrower (Figs. 8A, B).

Head much wider than long, fused with first pereomere. Antennae 1 and 2 (Fig. 8C) of three and seven segments respectively, both bearing many setae on distal segments. No eyes.

Pereon broadest, but only slightly so, across second and third pereomeres. All pereomeres separated by lateral incisions. Pereopods (Figs. 8D, E) all of same size, dactyli progressively smaller and carpi larger posteriorly.

Pleon about $\frac{1}{4}$ length of body, tapering to blunt point. No segments, but undulating margins indicating traces of segments. Appendages lacking. Ventral surface (Fig. 8F) bearing tiny paired slitlike markings.

Variations: Several males have their heads distinctly separated from their pereons, while the pleons of some are quite wide relative to pereonal width. In some cases (Fig. 8G) both of these variations occur.

Etymology.—The specific name *hyphalus* is the Latinized form of a Greek word meaning "submerged" in reference to the consistent occurrence of this species in much deeper water than *S. hyptius*.

Remarks.—*Stegophryxus hyphalus* differs from the other two species of the genus in several respects. The female is similar to that of *S. hyptius*, from which it differs in lacking eyes at all stages, having a much more symmetrical brood pouch, smaller uropods in the adult, more prominent pereopodal coxal plates, shorter pleomeres, and smaller pleonal lateral plates in immature forms. The adult female of *S. hyphalus* differs from that of *S. thompsoni* in having a relatively shorter head and pleon, more broadly pointed first oostegites, less conspicuous pereopodal coxal plates, narrower pleonal lateral plates and pleopodal rami, and much smaller uropods. Males of *S. hyphalus* differ from those of *S. hyptius* in lacking eyes, having pereomeres more strongly separated, and pleon longer, more pointed, and with more undulate margins. The male of *S. hyphalus* may be distinguished from that of *S. thompsoni* by its shorter head and pointed pleon. It is entirely possible that all three species have eyes in both sexes; eyes have been observed only in live or freshly preserved specimens of *S. hyptius*.

The only previous record of a *Stegophryxus* from the coast of California is that listed by Menzies and Miller (1954), who identified the host as a "*Pagurus sp.*" Their key to species indicates that they did indeed have a *Stegophryxus*; most likely *S. hyphalus*. Unfortunately, they list no locality or source for this record.

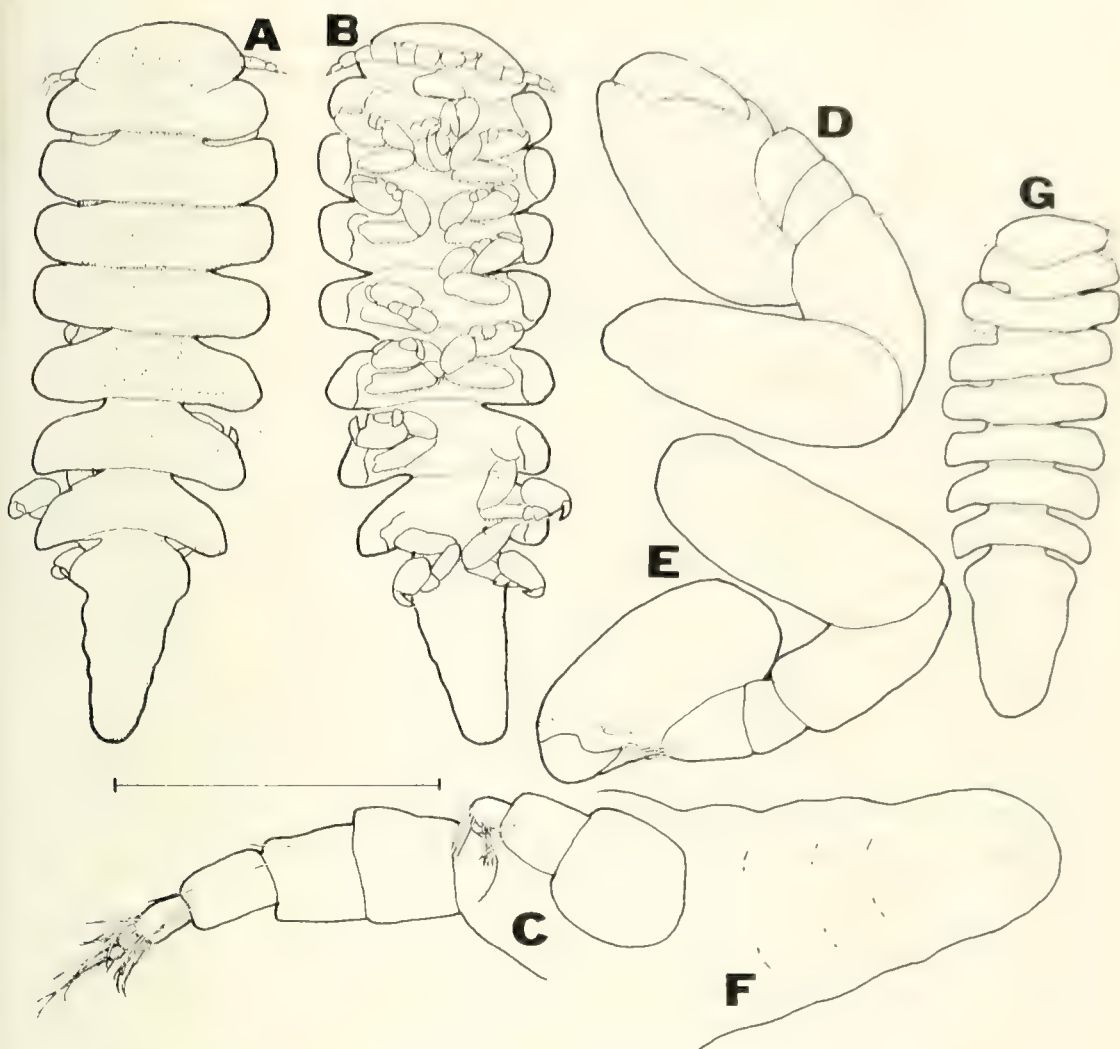


Figure 8. *Stegophryxus hyphalus*, new species. A-E, allotype male. G, second male. A. Dorsal view. B. Ventral view. C. Right antennae. D. Right pereopod 2. E. Right pereopod 7. F. Pleon, ventral view. G. Dorsal view. Scale indicates 1.0mm for A, B. G. 0.2mm for C, D, E, 0.4mm for F.

DISCUSSION

With the description of three species of *Stegophryxus*, it now becomes possible to provide a generic description, thus: *Female*. Body longer than broad, bent to left so right side is longer; head roughly pyriform with subparallel sides, produced into point anteriorly, indented postero-dorsally; first three pairs of oostegites arching far over head, others forming voluminous but tightly closed brood pouch; fifth oostegites much the largest, covering at least half of pereon

ventrally and produced posteriorly into lateral sacs, that on right side extending slightly to greatly posteriorly. First five pereomeres bent around and enclosing head; sixth pereomere much the largest, concave both anteriorly and posteriorly. First two pereopods anterior to head, second two beside it; first five pereopods clustered forward, sharply reflexed, last two far back, more or less straight. Pleon of six pleomeres. First five pleomeres bearing biramous pleopods and lateral plates ranging from linear-lanceolate to subovate by species, all from common peduncle so pleopods

appear "triramous." Terminal pleomere with uniramous bulbous uropods, ranging, by species, from button-like structures to large clubs. *Male*. Body length about three times width, sides nearly parallel except for head and pleon. Head more than twice as wide as long, smoothly rounded anteriorly, usually set off from pereon, or at least lateral indentations indicating separation. All pereomeres separated by deep lateral incisions. Pleon from $\frac{1}{3}$ to $\frac{1}{2}$ total body length, a single fused piece which is narrower than last pereomere, broadest behind anterior edge, rounded to pointed posteriorly. No pleonal appendages.

Three other genera are closely related to *Stegophryxus*, their females being distinguishable from those of *Stegophryxus* by several characters. In *Stegias* Richardson, pereomere 5 is longest, the last oostegites are not produced into posterior sacs, the pleon is relatively much shorter and broader, and the fourth and fifth pleomeres lack lateral plates. There are no markedly elongate pereomeres in females of *Anathelges* Bonnier, the body is nearly as broad as long, and the brood pouch symmetrical. In females of *Pseudostegias* Shiino, the brood pouch does not extend beyond the head, and only the first four pleomeres bear lateral plates. The males of these four genera are more difficult to separate along generic lines.

The distribution and host selection of the species of *Stegophryxus* are quite peculiar. First, this is evidently the only bopyrid genus found on both sides of the Americas and nowhere else. *Stegophryxus hyptius*, throughout its range, infests those species of *Pagurus* which occur on intertidal or shallow subtidal sandy bottoms, even though this range, in covering latitudes from about 26°N to 42°N, goes from an essentially tropical environment to nearly arctic environment. The distribution of *S. hyphalus* is completely different. It infests both known species of the pagurid genus *Parapagurodes* from a depth of 69 to 391m; and thus occurs nowhere close to the intertidal zone. Though the recorded latitudinal range of *S. hyphalus* is from 26°17'N to 36°27'N, there is little difference in temperature at the depths in question. The host and collection depth of *S. thompsoni* are unknown. In their description of this species, Nierstrasz and Brender à Brandis (1931) report: "Valparaiso. Krøyer. Ein Weibchen mit Männchen auf *Pagurus* sp." The label with the types bears the notation "af Pagurid," i.e., "from [a] pagurid," so the genus (and possibly even the family) of the host is uncertain. Janet Haig has kindly examined several

pagurids and diogenids collected off Chile and Peru and reports that none bore any abdominal parasites. As observed in a discussion of *Parathelges* spp. (Markham, 1972), there seems to be little host specificity among athelgine bopyrids. Therefore, it would be impossible to judge what the host of the types of *S. thompsoni* might have been even if more specimens should turn up.

ACKNOWLEDGMENTS

Edward B. Hatfield collected and provided to me a number of parasitized hermit crabs from the Miami area. Richard W. Heard provided hermit crabs which he and Charles Kellogg had collected in Georgia and North Carolina, while the latter provided collection data from some of them. Torben Wolff allowed me to examine the types of *S. thompsoni*. Janet Haig examined hermit crabs from Chile and Peru in the Allan Hancock Foundation collections, furnished collection data on the hermit crabs from California and granted me permission to describe their parasites. Patsy A. McLaughlin identified these crabs and made their parasites available to me as well as identifying many of the crabs collected along the Atlantic coast. Thomas E. Bowman and Lowell P. Thomas critically reviewed the manuscript. This is publication No. 1734 of the Rosenstiel School of Marine and Atmospheric Science, University of Miami, and No. 1 of the Arch Cape Marine Laboratory, Arch Cape, Oregon 97102.

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COMPARATIVE STUDY OF THE LANCETS AND SHEATHS OF SOME ACULEATE HYMENOPTERA

DENNIS M. POORE¹

ABSTRACT: A comparative study was made of the stinging apparatus of 102 species of aculeate Hymenoptera from the following families: Scoliidæ, Vespidae, Eumenidae, Pompilidae, Sphecidae, Andrenidae, Halictidae, Megachilidae, Anthophoridae, and Apidae. Analysis was confined to the presence or absence of barbs: number, arrangement, and types of barbs. The sheaths were compared as to the types of setae and the presence or absence of segmentation.

The purpose of this investigation was to compare the anatomical features of the lancets (first valvulae) and sheaths (third valvulae) of the stinging apparatus of some aculeate Hymenoptera. The differences found may be of importance in systematics, phylogeny, and contribute information on sting anatomy.

Morphological studies have been made on the stinging apparatus, but with little emphasis on the piercing structures and sheaths. *Dasymutilla occidentalis* (Mutillidae) possesses six barbs on each lancet (Hermann, 1968). *Polistes exclamans* and *P. annularis* (Vespidae) possess small barbs on their lancets (Hunt and Hermann, 1970). In 1967 Hermann and Blum reported that the presence or absence of barbs on the lancets of formicids had little significance because there is no constant pattern. Using high magnification, Smith (1970) noted that *Myzinum maculatum* (Tiphidae) possesses companiform sensilla (sensory pores) and serrulea (subdivisions of the barbs into small projecting teeth). Sheath segmentation was noted by Hazeltine (1967), but little practical application was made of it as far as length ratios of the segments and setae types present.

METHODS

Stings were extracted from preserved specimens, dehydrated in three solutions (80, 95, and 100 percent) of ETOH, cleared in toluene, and mounted on slides using piccolyte as a mounting medium.

RESULTS AND DISCUSSION

Only one species, *Anthophora curta*, of the 102 observed lacked barbs. Barbs have been categorized into five types (Fig. 1A-E): acute; saw-

toothed; rounded; knobbed; and reduced. Barbs with an angle of less than 75 degrees were classified as acute; those with an angle of greater than 75 degrees were classified as saw-toothed. Single saw-toothed barbs were prevalent in pompilids. Rounded barbs were confined to scoliids and the tribe Sphecini (Sphecidae). Reduced barbs were found in specimens of *Andrena prunorum*. Knobbed barbs were confined to the tribe Ammophilini.

In some genera, *Auplopus*, *Ceratina*, *Euodynerus*, *Lasioglossum*, and *Stenodynerus*, the number of barbs remained constant. In others the number of barbs varied, but a typical number of barbs for those genera was evident. In some species the number of barbs varied from the typical number, but the range never exceeded plus or minus one barb.

The *Apis mellifera* queen had a reduced number of barbs as compared to the workers, possibly a survival adaptation. The queens of *Vespula pensylvanica* and *V. sulphurea* possessed one more barb than the worker. This may be due to increased size and lack of sting autotomy. The barb type, size, and number found in *Apis* workers and in *V. pensylvanica* and *V. sulphurea* were comparable, suggesting that some other mechanism (possibly a difference in muscular attachment between the sting and the abdomen) must be responsible for the sting autotomy found in the *Apis* workers.

Barbs were arranged on the lancet in a linear fashion and were of one type per species with the following exceptions: *Tachysphex ashmeadii*, in which the first six barbs at the distal end of the lancet were acute with the remaining five proximal barbs smoothed off into minute knobs:

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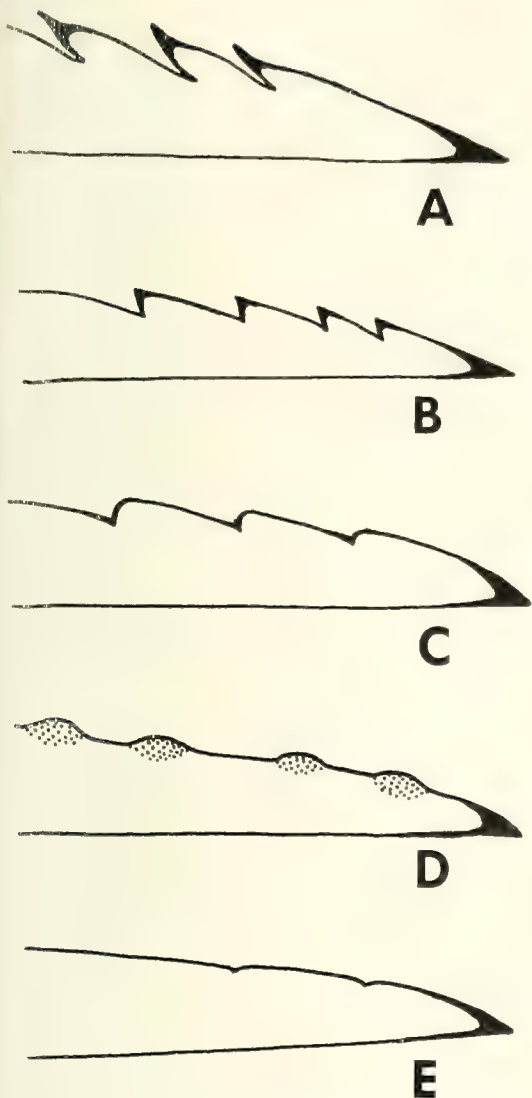


Figure 1. Lancets of some aculeate hymenopterans. A, Acute barbs of *Apis mellifera* worker 450 $\times$; B, Saw-toothed barbs of *Ancistrocerus abdiatus cytainus* 535 $\times$; C, Rounded barbs of *Campsomeris tolteca* 450 $\times$; D, Knobbed barbs of *Ammophila aberti* 450 $\times$; E, Reduced barbs of *Andrena prunorum* 535 $\times$.

Prionyx foxi, in which the first five barbs at the distal end of the lancet were rounded with the remaining six proximal barbs smoothed off into minute knobs; *Centris rhodopus*, in which the most common barb arrangement, from distal to proximal, was one acute barb followed by two adjacent acute barbs and finally another acute barb; *Centris pallida*, in which the most common barb arrangement, from distal to proximal, was one acute barb followed by two sets of two ad-

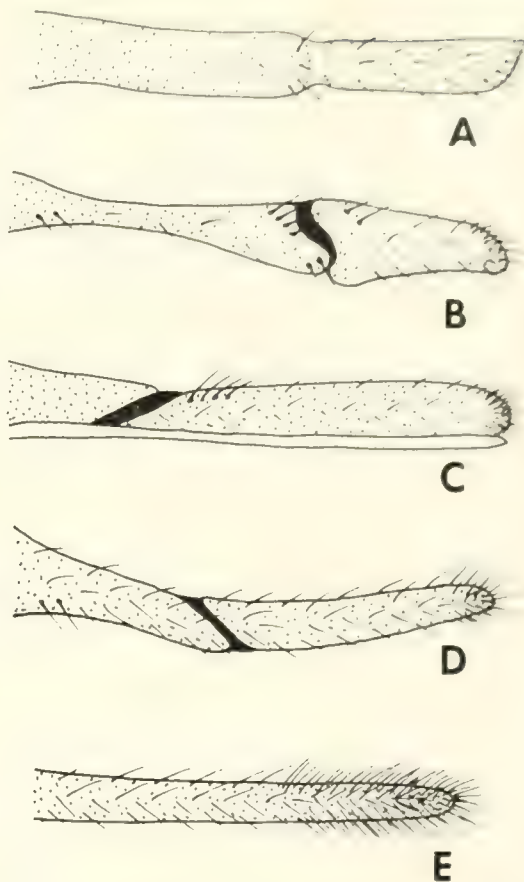


Figure 2. Sheaths of some aculeate hymenopterans. A, Constricted sheath of *Ancistrocerus abdiatus cytainus* 85 $\times$; B, Basal segment twice the length of the second segment, *Anoplius americanus ambiguus* 50 $\times$; C, Basal segment $\frac{1}{2}$ the length of the second segment, *Campsomeris tolteca* 35 $\times$; D, First and second segments of approximate equal lengths, *Sceliphron caementarium* 50 $\times$; E, Unsegmented sheath of *Coelioxys obtusiventris* 50 $\times$.

jacent acute barbs: *Clypeadon utahensis*, in which there were two acute barbs at the distal end, two sets of two adjacent acute barbs, and three acute barbs proximally. Most specimens studied from the subfamily Halicinae had the same number of barbs and the same barb arrangement: Two acute barbs at the distal end, two sets of two adjacent acute barbs, and one acute barb proximally.

Sheaths were found to be of three basic types: Constricted, two-segmented, and unsegmented. Annulated constrictions (Fig. 2A) were found in the sheaths of Eumenidae and were less pronounced and appeared as a light band with minimal constriction in Vespinae. In the constricted

[illegible]

TABLE 1. (Continued)

Species Examined	ST	BT	Number of Barbs per Lancelet											
			0	1	2	3	4	5	6	7	8	9	10	11
Sphecini (continued)														
<i>Prionyx parkeri</i> (Boh. & Menke)	D	C					2							
<i>Sphex ashmeadi</i> (Fernald)	C	C				5	1							
<i>Sphex ichneumoneus</i> (L.)	C	C				4								
EUMENIDAE														
<i>Ancistrocerus abdiatus cytainus</i> (Cam.)	A	B					4							
<i>Ancistrocerus spilogaster</i> (Cam.)	A	A						2						
<i>Ancistrocerus tuberculiceps sutterianus</i> (Sauss.)	A	A						4						
<i>Eumenes crucifera</i> Prov.	A	A					2	8						
<i>Euodynerus annulatum</i> (Say)	A	A						10						
<i>Euodynerus foraminatus blandinus</i> (Rohw.)	A	A						2						
<i>Euodynerus foraminatus scutellaris</i> (Sauss.)	A	A						4						
<i>Euodynerus hidalgo vierecki</i> (Cam.)	A	A						2						
<i>Euodynerus pratense</i> (Sauss.)	A	A						4						
<i>Leptochilus propodealis</i> Boh.	A	A			2									
<i>Pterochilus morrisoni</i> Cress.	A	A					2							
<i>Stenodynerus acarigaster</i> Boh.	A	A					2							
<i>Stenodynerus microstictus</i> (Vier.)	A	A					2							
<i>Stenodynerus toltecus</i> (Sauss.)	A	A					2							
VESPIDAE														
Polybiinae														
<i>Epipona tatua</i> Guerin	E	A								15	9			
<i>Mischocyttarus flavitarsis</i> (Sauss.)	E	A				2	30							
Polistinae														
<i>Polistes annularis</i> (L.)	E	A								1	11			
<i>Polistes apachus</i> Sauss.	E	A						30	2					
<i>Polistes carolinus</i> (L.)	E	A						12	12					
<i>Polistes dorsalis californicus</i> Boh.	E	A						17	7					
<i>Polistes exclamans</i> Vier.	E	A							31	11				
<i>Polistes fuscatus aurifer</i> Sauss.	E	A					9	21						
<i>Polistes fuscatus variatus</i> Cress.	E	A					3	19						
<i>Polistes metricus</i> Say	E	A						10	2					
Vespinae														
<i>Vespula maculifrons</i> (Buysson)	A	A									10	14		
<i>Vespula maculata</i> (L.)	A	A								5	43			
<i>Vespula pensylvanica</i> (Sauss.) queen	A	A											1	25
<i>Vespula pensylvanica</i> (Sauss.) worker	A	A										7	21	
<i>Vespula sulphurea</i> (Sauss.) queen	A	A												4
<i>Vespula sulphurea</i> (Sauss.) worker	A	A											4	2
ANDRENIDAE														
Andreninae														
<i>Andrena cerasifolii</i> Ckll.	E	A			8	2								
<i>Andrena prunorum</i> Ckll.	E	E			20									
HALICTIDAE														
Halictinae														
<i>Agapostenom</i> sp.	E	A									6			
<i>Augochlora cuprea</i> (Sm.)	E	A								3	21			
<i>Augochlorella pomoniella</i> Ckll.	E	A									2			
<i>Halictus farinosus</i> F.Sm.	E	A									9	1		
<i>Halictus ligatus</i> Say	E	A								3	17			
<i>Lasioglossum mellipes</i> (Crawford.)	E	A									6			
<i>Lasioglossum sisymbrii</i> (Crawford.)	E	A									2			

TABLE 1. (Continued)

Species Examined	ST	BT	Number of Barbs per Lancet											
			0	1	2	3	4	5	6	7	8	9	10	11
MEGACHILIDAE														
Lithurginae														
<i>Lithurgus apicalis</i> (Cress.)	E	A				3	5							
Megachilinae														
Anthidiini														
<i>Anthidium collectum</i> Huard	E	A								2				
<i>Callanthidium illustre</i> (Cress.)	E	A								2				
Megachilini														
<i>Ashmeadiella opuntiae</i> (Ckll.)	E	A							1	1				
<i>Chalicodoma occidentalis</i> Fox	E	A										2		
<i>Coelioxys obtusiventris</i> Crwfd.	E	A											2	
ANTHOPHORIDAE														
Anthophorinae														
Anthophorini														
<i>Anthophora curta</i> Prov.	E	—	2											
Emphorini														
<i>Diadasia australis</i> (Cress.)	C	A				2	4							
<i>Diadasia australis californica</i> Timb.	C	A				20								
<i>Diadasia enavata</i> (Cress.)	C	A				2								
<i>Diadasia laticauda</i> Ckll.	C	A				14	4							
<i>Diadasia rinconis</i> Ckll.	C	A				6								
Eucerini														
<i>Melissodes</i> sp.	C	B			8									
Nomadini														
<i>Nomada formula</i> Vier.	E	C			2									
Centridini														
<i>Centris pallida</i> Fox	E	A					4	8	2					
<i>Centris rhodopus</i> Ckll.	E	A					18	2						
Xylocopinae														
Ceratinini														
<i>Ceratina acantha</i> Prov.	E	A			4									
<i>Ceratina punctigena</i> Ckll.	E	A			2									
Xylocopini														
<i>Xylocopa brasilianorum varipuncta</i> Patton	E	A			4	26								
<i>Xylocopa virginica</i> L.	E	A				36	8							
APIDAE														
Apinae														
Apini														
<i>Apis dorsata</i> Fab.	E	A											36	8
<i>Apis florea</i> Fab.	E	A											45	3
<i>Apis indica</i> Fab.	E	A											45	1
<i>Apis mellifera</i> L. queen	E	A					15	26	1					
<i>Apis mellifera</i> L. worker	E	A											28	2
Bombini														
<i>Bombus californicus</i> F.Sm.	E	A						8						
<i>Bombus edwardsii</i> Cress.	E	A						12						
<i>Bombus morrisoni</i> Cress.	E	A						4						
<i>Bombus sonorus</i> Say	E	A						8						
<i>Bombus vandykei</i> (Frison)	E	A						9	1					

sheaths, the basal segment was slightly longer than the second segment.

Sheaths with two segments (Fig. 2B-D) were observed in species of sphecids, pompilids, scoliids, and in the tribes Emphorini and Eucerini (Anthophoridae). Unsegmented sheaths (Fig. 2E) were present in all other species.

Two-segmented sheaths were of three basic types. Sheaths with the basal segment twice the length of the second segment (Fig. 2B) were confined to the pompilids. Sheaths with the second segment twice the length of the basal segment (Fig. 2C) were found in scoliids and in the tribes Philanthini (Sphecidae) and Emphorini (Anthophoridae) and scattered throughout other groups. Two-segmented sheaths with the segments approximately equal in length (Fig. 2D) were found in the tribes Bembicini and Ammophilini (Sphecidae) and scattered throughout other groups. In the five species of *Diadasia* examined, the sulci were at approximately a 20 degree angle to the axis of the sheath, a more acute angle than on the other segmented sheaths with the second segment twice the length of the basal segment. Barbs and sheath characteristics, for all species examined are summarized in Table 1.

Plumose setae on the sheaths were present in all apoid species except *Lasioglossum sisymbrii*, *Nomada formula*, and *Apis* workers. The *Apis* workers had setae that were reduced in size. Simple setae were present in all other species.

In some species, only one specimen was studied. It would be desirable to examine more specimens, including some from different geographical populations, to determine if the anatomical features remain constant for those species. In addition, more species within certain groups (genera, tribes,

et cetera) should be studied to determine results obtained for each species in this study hold true for its entire group.

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A NEW SPECIES OF *CLYMENELLA* (POLYCHAETA: MALDANIDAE) FROM TOMALES BAY, CALIFORNIA

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ABSTRACT: A new species of *Clymenella* is described from shallow subtidal sediments in Tomales Bay. Comparisons are made with related *Clymenella* species.

Four specimens of an unknown species of *Clymenella* were collected at a depth of about one meter during a low tide in White Gulch, Tomales Bay, California on 22 October 1969. The specimens could not be identified as any species of *Clymenella* known from California (Hartman, Atlas of the sedentariate polychaetous annelids from California, Allan Hancock Foundation, Los Angeles, 1969) and were determined to represent a previously undescribed species. This is contribution number 33 from the Pacific Marine Station.

Clymenella californica, new species

Figures 1 and 2

Material examined: White Gulch, Tomales Bay, California, 22 October 1969, from loose silt sediment, depth about one meter; four specimens, holotype and three paratypes, deposited in the collections of the Allan Hancock Foundation, University of Southern California.

Description: The specimens have from 22 to 27 setigerous segments with one preanal asetigerous segment in addition to the peristomial and pygidial segment. The holotype has 27 setigerous segments, measures 200 mm in length and 2 mm in width. Individual posterior segments are greatly prolonged and maximally measure up to 17 mm in length while those from anterior setigers measure 2.5 to 3 mm.

The anterior end terminates in an elongated ce-

phalic plaque which has an anterior projecting palpode, followed posteriorly on each side by raised lateral margins which surround the plaque and merge posteriorly (Figs. 1a-1b). The margin is interrupted by small notches near the posterior end of the plaque. Two parallel nuchal grooves lie alongside an elevated nuchal ridge which extends through the mid-region of the plaque. Clusters of eyespots occur on the anterior lateral edge of the prostomium (Fig. 1a).

The first three setigers lack collars, but bear fascicles of long capillary notosetae and one or two acicular neuropodial spines (Fig. 2a). Setiger 4 has a conspicuous smooth collar on its anterior border. Notosetae are capillaries, but the neurosetae consist of about fifteen non-bearded rostrate setae, each of which has a main fang and four secondary teeth (Fig. 2b). Setiger 5 and succeeding setigers bear notopodial capillary setae and bearded rostrate neurosetae (Fig. 2c). The number of secondary teeth gradually increases from four to five. The setal fascicles gradually shift from dorsolateral positions in anterior segments (Fig. 1a) to lateral positions in posterior segments (Fig. 1c).

The anal funnel terminates in a ring of 22 nearly equal cirri (Figs. 1c-1d). The anus is at the apex of a raised cone.

Color of the first three setigers is iridescent pink;

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TABLE 1. Differential characteristics of California *Clymenella* species.

Characteristics	<i>C. californica</i>	<i>C. complanata</i>
Number of setigers	22-27 setigers and 1 asetiger	21 setigers and 4 asetigers
Length	200 mm	90 mm
Transverse nuchal groove across plaque	absent	present
Marginal flange around plaque	present	absent
Segmental collar	setiger 4	setigers 4 and 5
Habitat	silty sediments in Tomales Bay	shaley rock crevices of the open coast

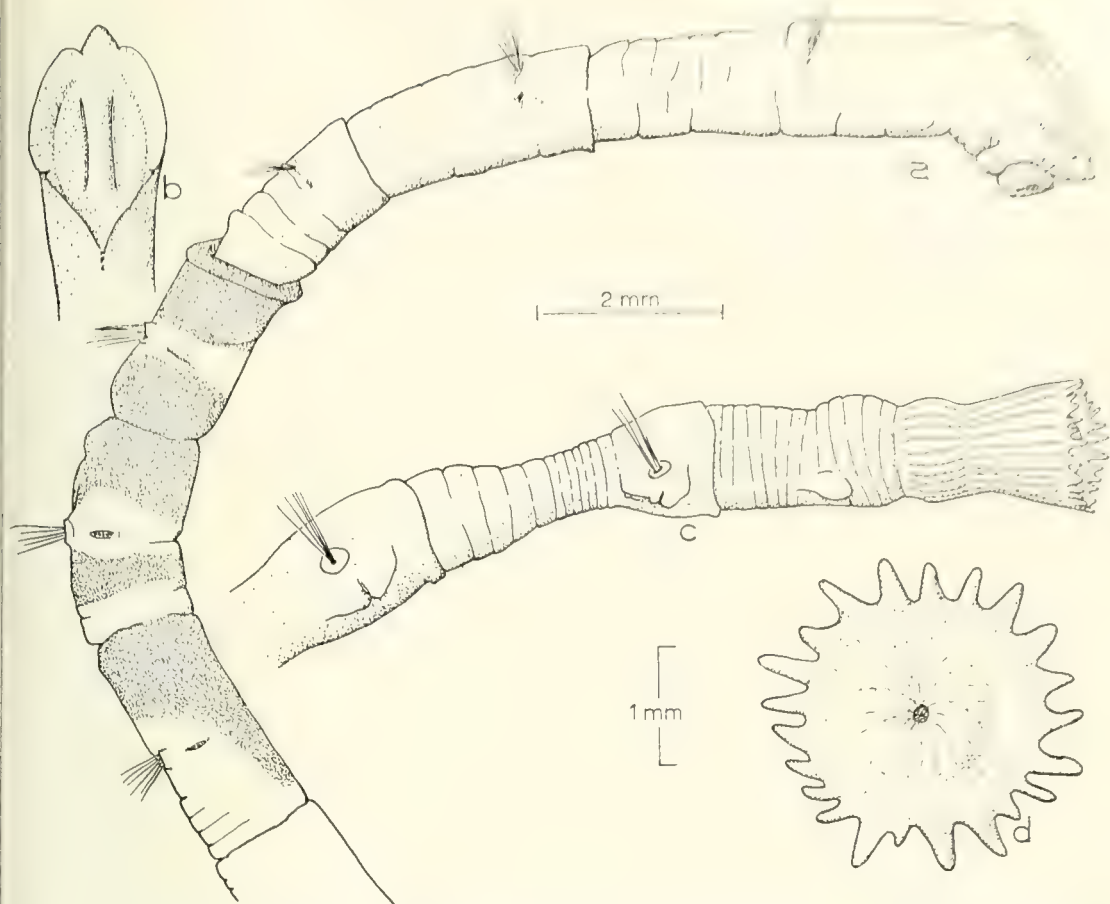


Figure 1. *Clymenella californica*, new species: a, anterior end in lateral view; b, cephalic plaque in dorsal view; c, posterior end in lateral view; d, pygidium in posterior view.

setigers 4-7 have deeply pigmented red areas alternating with the lighter pink bands; setigers 8-13 are pale brown to white (white when sexually mature); the remaining segments exhibit color gradients from light to dark orange. The entire body surface is covered with numerous lines and folds.

The tube is rigid, J-shaped, and formed of cemented sand grains.

Distribution: Tomales Bay, California.

Remarks: *Clymenella californica* differs considerably from *C. complanata* (Hartman, 1969) which is known only from San Mateo County and Point Conception in California where it inhabits shaley rocks from the intertidal to shallow subtidal. See table 1 for differentiating characteristics. On a global basis, *Clymenella californica* appears closest in morphology to *C. cincta* (St. Joseph, 1894) from France. It differs from *C. cincta* in having its collar margin entire instead of incised. The nuchal slits of *C. californica* are

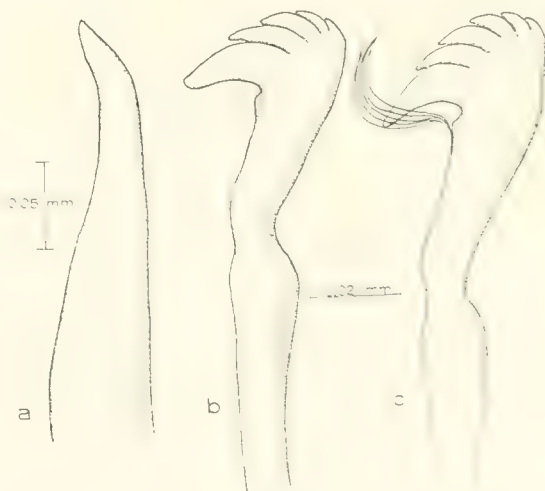


Figure 2. *Clymenella californica*, new species: a, acicular seta from setiger 1; b, rostrate seta from setiger 4; c, rostrate seta from setiger 21.

parallel, but transverse in *C. cincta*. Non-bearded rostrate neurosetae present in *C. californica* are not reported for *C. cincta*. The number of setigers is not known.

Clymenella californica is superficially confused with *Axiothella rubrocincta* (Johnson, 1901), a common maldanid in north Pacific bays and estuaries. The generic differences involve the presence of thick acicular neuropodial spines in

setigers 1–3 of *Clymenella* where *Axiothella* has rostrate neurosetae.

Biology: The functional morphology of feeding in *Clymenella californica*, *Axiothella rubrocincta*, and *Praxillella affinis pacifica* has been studied and will be published elsewhere (Kudenov, M.S.). Eggs were present in the coelom of some specimens of *C. californica*.

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RESEARCH NOTES

NOTES ON THE ARBOREAL ACTIVITIES OF *PEROMYSCUS BOYLI* IN INYO COUNTY, CALIFORNIA

Arboreal activities in various species of *Peromyscus* have been known for many years (Baker, 1968). Although the arboreal tendencies of *Peromyscus boylii* have been noted by Bailey (1932), Cahalane (1939), Long (1961), and Storer, Evans, and Palmer, (1944), comprehensive studies of this aspect are unknown to the author. Studies of home ranges, population densities, and other aspects of their life histories were made by Drake (1958), Long (1961), and Storer *et al.*, (1944).

During the summer of 1971, while doing field work in the Owens Valley of California, the author established a base camp at Cottonwood Creek Campground, 11 miles north and 4 miles west of Olancho, Inyo County. In the evenings, mice were observed in the canyon live oaks (*Quercus chrysolepis*). An attempt to study the arboreal habits of these mice, subsequently identified as *Peromyscus boylii rowleyi*, was initiated.

The dominant tree in Cottonwood Canyon was the canyon live oak. There were also a few scattered pinyon pines (*Pinus monophylla*). Cottonwoods (*Populus fremontii*) were present only along the immediate stream side. Shrubs were common in the areas between the oaks; these were, in order of decreasing abundance: basin sagebrush (*Artemisia tridentata*), wingscale (*Atriplex canescens*), and rabbit brush (*Chrysothamnus nauseosus*).

Two canyon live oaks were selected as the site of study. A Sherman live trap was placed on each of the main branches and five traps were placed at the base of the trees. The traps were baited with rolled oats in the evenings and emptied each morning. Trapping in the oak trees was continuous from 13 August to 26 August 1971. A total of 14 nights with 196 trap-nights was recorded. Also, a single trapline,

(20 trap stations set 25 feet apart with 10 traps per station) was set on the canyon floor. The trapline was maintained for four nights (13-16 July 1971) in a shrub area, approximately 100 feet from the two oak trees.

Live caught mice were toe clipped (Burt 1940). Sex and age data were recorded for each mouse; it was released upon the same branch from which it was originally captured. Ages of mice were determined from pelage color as follows: adults, full-adult color; subadults, showing some adult color but with post-juvenile molt incomplete; and juveniles, with dull grey pelage apparent and no indication of molt.

In the trees, 34 *P. b. rowleyi* were captured 95 times. Adult and subadult female mice were more often captured than were any males or juvenile females (Table 1). Ground trapping for four days yielded nearly equal numbers of male and female mice of all age classes. Capture data for ground trapping was as follows: day 1, seven males and six females; day 2, five males and four females; day 3, four males and four females; day 4, four males and four females. Sex ratios for both tree and ground trapping are recorded in Table 2.

A statistically significant difference ($\chi^2 = 3.98$, 1 DF, < 0.05 level) was found to exist between the sex ratios of tree and ground trapped mice. Females are apparently more prone to foraging in trees than are male mice, resulting in more captures of females than males. Though the combined number of females captured was greater than males, there was not a significant difference in the total sex ratio ($\chi^2 = 2.06$, 1 DF, > 0.05).

A season of increased activity (June-August) was recorded for the brush mouse in the Sierra Nevada of California by Storer *et al.*, (1944). They believed that this increased activity caused a decrease in the food supply, thus forcing the mice to forage in trees. Long (1961) indicated that brush mice in Kansas

TABLE 1. Recapture data of *Peromyscus boylii rowleyi* (tree captures). Age classes are indicated as: A (adult); S (subadult); J (juvenile).

Times Captured	Males			Females		
	A	S	J	A	S	J
1	5	—	1	3	2	4
2	1	—	1	2	2	—
3	—	1	—	2	1	—
4	1	—	—	1	1	—
5	—	—	—	—	1	—
6	—	—	—	1	1	1
7+	—	—	—	1	1	—

TABLE 2. Sex ratio data for both trapping areas. The total number of mice for each age class is recorded. Ratio is recorded as males per female.

	Ad.	Subad.	Juv.	Totals
TREES				
Males	7	1	2	10
Females	10	9	5	24
Ratio	0.70	0.11	0.40	0.42
GROUND				
Males	7	10	3	20
Females	7	9	2	18
Ratio	1.0	1.11	1.50	1.11

seemed to prefer acorns as a food item. In the present study, the fact that female mice were more commonly taken in the oak trees than were males may be due to competition with the males on the ground. This competition may force the females to utilize an alternative food source in the trees.

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NOTES ON SOME BATS FROM A CAVE ON PENINSULA PARAGUANA, VENEZUELA

Cueva del Guano is a limestone cave located on the Peninsula Paraguana, 58 km N and 34 km W of

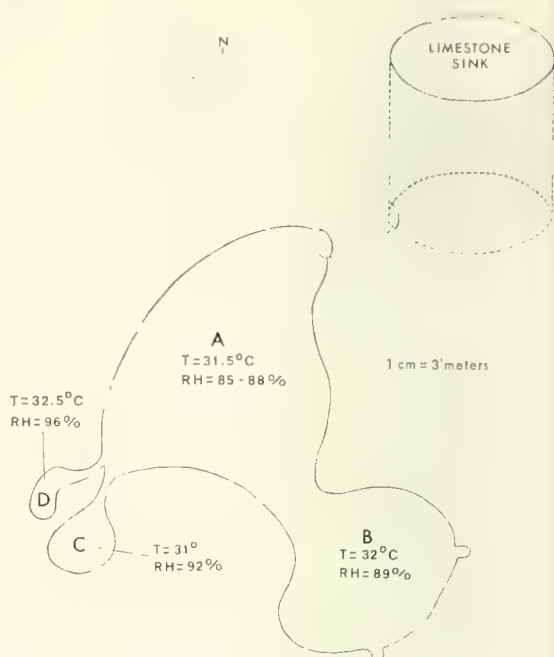


Figure 1. Diagrammatic sketch of Cueva del Guano showing the positions and sizes of the four rooms with temperatures and relative humidities.

Coro, Falcon, Venezuela. The entrance to the cave is about 12 meters below the surface of the ground, in a limestone sink (Fig. 1).

The authors visited the cave to obtain bats on July 10, 11, 22, 23, 27, and 31, 1968. Temperatures and relative humidity readings were recorded for each room on July 22, 23, and 31 (Fig. 1). The outside temperature and relative humidity varied from 28.5°-31° C and 58-66.5 percent, respectively.

Representatives of five species of bats were captured in the cave. These were: *Pteronotus davyi*, *P. parnellii*, *Mormoops megalophylla*, *Leptonycteris curasoae*, and *Natalus tumidirostris*. This represents the first record of *L. curasoae* from the Venezuelan mainland of South America. In the cave, 75 specimens (65 ♂ and 10 ♀) of *L. curasoae* were obtained. Also, 34 specimens (7 ♂ and 27 ♀) of this species were netted in the xeric thorn forest, which was the dominant vegetation of the peninsula (the net area was about 9 km S of the cave). These specimens are now deposited in the United States National Museum of Natural History (catalog numbers: 444758-444819 and 491749-491794); eventually a share of the collection will be returned to Venezuela.

This species was first reported (as *L. nivalis*) from the Colombian mainland of South America by Marinkelle and Grose (Nature, 218(5140):487, 1968). Subsequently, other specimens were reported from a second locality, also in Colombia (Marinkelle and Cadena, Mammalia, 36:50-58, 1972).

The maximum number of bats in Cueva del Guano was estimated to be between 45,000 and 50,000 individuals. This estimate was determined from a photographic slide, from which we were able to count the number of bats (mostly *P. davyi*) roosting per sq m on the ceiling in room A. This room contained the greatest number of bats, 65 per sq m or approximately 30,000 individuals. Overall, *L. curasoae* and *P. davyi* were the most abundant, while *P. parnellii*, *M. megalophylla*, and *N. tumidirostris* were considerably fewer in number.

On July 10 and 11, *L. curasoae* was estimated to be about five times as abundant as *P. davyi*. However, on subsequent visits, individuals of *P. davyi* were more numerous than they had been, *L. curasoae* being considerably less abundant. In fact, on 27 July only one *L. curasoae* was taken, and by 31 July they were not observed at all. It is interesting to note that *P. davyi* was also recorded to show temporal alternations of abundance with other bats in a Mexican cave (Dalquest and Hall, J. Mamm., 30:423-427, 1949). It is possible that *L. curasoae* and *P. davyi* range over large areas, alternately roosting at different localities.

Leptonycteris curasoae, *P. davyi*, and *P. parnellii* were apparently roosting together on the ceiling in rooms A and B. *Mormoops megalophylla* were taken only from small crevices in the ceiling or on the walls in rooms A, B, and C. *Natalus tumidirostris* was the only species found in room D. In this room we recorded the highest temperature and relative humidity for the cave (Fig. 1). *Natalus tumidirostris* was also captured in room B, from small crevices where the humidity and temperature felt, to our hands, to be higher than in the center of the room. *Natalus tumidirostris* was reported to prefer the driest parts of warm, humid caves in Trinidad (Goodwin and Greenhall, Bull. Amer. Mus. Nat. Hist., 122: 187-302, 1961). However, in that paper the actual temperatures and humidities were not recorded. Therefore, a direct comparison is not possible. It may be that *N. tumidirostris* is forced into the more humid areas of Cueva del Guano because of crowding by the other species of bats.

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TANTILLA TAENIATA (BOCOURT) ADDITION TO THE SNAKE FAUNA OF EL SALVADOR

Tantilla taeniata (Bocourt), a relatively widespread member of the genus, is known to occur from southeastern Oaxaca, México to central Nicaragua (Wilson and Meyer, Herpetologica, 27:11-40, 1971; Wilson and Hahn, Bull. Florida St. Mus., 17:93-150, 1973; Wilson and Villa, Bull. So. California Acad. Sci., 72:93-96, 1973). This species has not been recorded from El Salvador, however, and this paper documents its occurrence there.

Tantilla taeniata is known from relatively few specimens (12 to date), and it appears that almost every specimen collected since the last review is contributing markedly to the expansion of the diagnosis of this species. The present specimen is no exception.

The specimen of *T. taeniata* from El Salvador (University of Utah 4716) was collected at an elevation of 1000 m on Volcán de Conchagua, 4 km S La Unión, Depto. La Unión. It is a female with the following characteristics: 143 ventrals (this count is probably ± 1 scale from the actual number because several ventrals are missing; I made the count by shifting to the lowermost dorsal scale row to skirt that point); tail incomplete; dorsal scale rows 15-15-15; anal plate single (all *Tantilla*, of course, characteristically have a divided anal plate); supralabials 7-7 (3rd and 4th entering orbit); infralabials 6-6, first pair not in medial contact, 4 in contact with anterior chin shields; preocular single and in contact with postnasal; postoculars 2-2; temporals 1+1.

The dorsum is brown and the pale stripes are tan edged with dark brown. The middorsal pale stripe occupies the middorsal scale row and the adjacent halves of the paravertebral rows, and the lateral pale stripe occupies the adjacent halves of rows 3 and 4. Both stripes continue onto the tail. The anterior end of the middorsal stripe is separated by 4 scales from the nape band. The first dorsal scale row is divided into dark brown upper and cream lower halves. The venter is immaculate cream. The tan nape band is complete, covers the tips of the parietals and $1\frac{1}{4}$ scales posterior to the parietals, and crosses the posterior half of the last supralabial. Pre- and postocular pale blotches are present.

I have presented a relatively detailed description of the scutellation and color pattern of this specimen because it is peculiar in one respect and I need to justify my allocation of it to *T. taeniata*. The color pattern of UU 4716 is like that of all other specimens of *T. taeniata* that I have examined, especially with respect to the diagnostic characteristics of the species, viz., a pale middorsal stripe occupying the middorsal and adjacent halves of the paravertebral rows, a pale lateral stripe occupying the adjacent halves of rows 3 and 4, first scale row divided into dark upper and pale lower halves, and a complete nuchal collar crossing the last supralabial.

The ventral count (143), however, even though approximate, is well below the range for other known females of this species (158–178). This number of ventrals falls within the known range for females of *T. jani* (141–153) known from low and moderate elevations of the Pacific versant from eastern Oaxaca, México to Guatemala. In view of the fact that the ventral count of UU 4716 falls within the range for female *T. jani* and in view of the geographic intermediacy of this specimen (Wilson and Meyer, 1971), it is conceivable that *T. taeniata* and *T. jani* may be conspecific. I feel it premature, however, to make the necessary nomenclatural changes, as no other specimens are known from areas between the ranges of the two species. In addition, variation in scutellation in *T. taeniata* remains poorly known and there are distinct pattern differences between the two (Wilson and Meyer, 1971). For the time being, I will continue to consider *T. taeniata* and *T. jani* distinct species.

The specimen from El Salvador bears some re-

semblance to the holotype of *Leptocalamus trilineatus* Peters, the status of which has remained enigmatic since its description (Wilson and Meyer, 1971). The holotype of *L. trilineatus*, which I have examined previously, is a female with 149 ventrals, a count close to that of UU 4716, but there are important pattern differences between the two and they do not appear to belong to the same species. The holotype of *L. trilineatus* has a middorsal pale stripe confined to the middorsal row, the upper edge of the pale lateral stripe is not outlined with dark pigment, and there is no continuation of the middorsal and lateral stripes onto the tail. The name *Leptocalamus trilineatus* still has questionable status.

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INSTRUCTIONS FOR AUTHORS

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A feature article comprises approximately five to thirty typewritten pages. Papers should be divided into the following sections: abstract, introduction, methods, results, discussion, and conclusions, acknowledgments, and literature cited. Avoid using more than two levels of subheadings.

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Brattstrom, B. H. 1969. The condor in California. Pp. 369-382 in Vertebrates of California, (S. F.

Payne, ed.), Univ. California Press, xii + 635 pp.

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COVER: *An extinct Diatom, Kittonia elaborata Grobe and Strut, from Eocene sediments of the Indian Ocean (magnified 500×).*

Photo by Dr. W. W. Wornardt, Union Oil Research, Brea, California.

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BULLETIN OF THE SOUTHERN CALIFORNIA
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VOLUME 73

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NUMBER 1

REPRODUCTIVE BEHAVIOR OF THE GRAY WHALE
ESCHRICHTIUS ROBUSTUS, IN BAJA CALIFORNIA

WILLIAM F. SAMARAS¹

ABSTRACT: Patterns of movement and repetitive behavior of gray whales in a specific area of Scammon's Lagoon suggest precopulative ritual. Individuals move into a specific area of the lagoon in the early morning and conspicuously engage in spyhopping, which is associated with the gray whale's courtship behavior. Whales expose their heads above the surface and remain motionless in this position for at least ten seconds before submerging. A lull in activity in the late morning and early afternoon is followed by intensified pairing and copulation.

Gray whales, *Eschrichtius robustus* (Lilljeborg, 1861), spend the summer months feeding primarily on amphipods and thereby acquire a thick blanket of blubber in the North Bering and Chukchi Seas in preparation for their four-month long, 7000 mile journey south to their winter quarters among the lagoons and shallow, protected bays of central and southern Baja California (Rice and Wolman, 1971). It is in these lagoons that most of the calving takes place. The gestation period for *E. robustus* is approximately 13 months with birth occurring from the middle of December into early February (Rice and Wolman, 1971). The round trip of eight months, beginning in October and ending in May, gives these whales the distance record for migrating mammals (Fig.1).

From 29 January to 2 February 1973, I observed gray whales in the Laguna Ojo de Liebre (also known as Scammon's Lagoon), which is one of the primary breeding and calving areas on the west coast of Baja California, Mexico, (Latitude 27°58' N, Longitude 114°16' W). Entrance to Scammon's Lagoon is from the north through a narrow, shallow channel averaging 4 fathoms in depth (Fig. 2a). The main channel is flanked by shallow bars whose presence is evidenced by onshore swells breaking over them. Soon after entering the lagoon at 0630 on 29 January spouting whales were sighted in every

direction. Within a period of 15 minutes it was estimated that there were in excess of 50 animals in an area of approximately one square mile. Because of the large assemblage of whales just inside the entrance bar, I designated it the staging area (Fig. 2b).

STAGING AREA BEHAVIOR

Most of the whales in the staging area appeared to be milling around without any general direction of movement, and most of those observed through binoculars were large, ranging in size from 30 to 40 feet in length. Prior observations by Scammon (1874) indicated that the preponderance of whales in this part of the lagoon are, in the main, unattached males, although it is not known how he determined this. It appears reasonable that this assemblage of whales also includes sexually mature or oestrative females. Most of the incoming, pregnant females enter the lagoon and continue into the calving area often referred to as the nursery (Fig. 2c).

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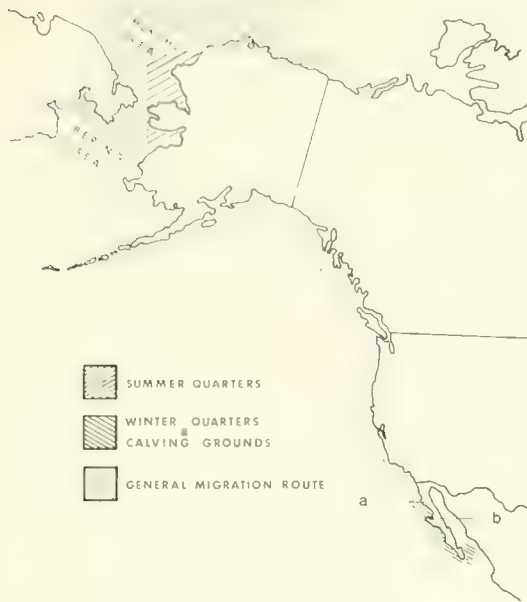


Figure 1. Seasonal distribution and migration route of the gray whale, *Eschrichtius robustus*: a, Baja California, Mexico; b, Scammon's Lagoon.

Respiratory-diving behavior.—Within the staging area, the whales were swimming slowly, exhibiting their typical respiratory-diving behavior, which is initiated by the crown of the head and paired blow-holes breaking the surface of the sea. Exhalation is signified by a visible, heart-shaped, vaporous spout and a very audible blow. The whale then begins to round-out, exposing its dorsum to at least the primary dorsal ridge (sometimes called the dorsal bump) then submerges a few feet beneath the surface for one to two minutes and again resurfaces to exhale and inhale. This procedure is repeated, on the average, three to four times. After the last blow in the respiratory series or blast, as it was called by whalers (Slijper, 1962), the round-out is much more pronounced and deliberate. The entire dorsum and caudal peduncle arches above the surface exposing its entire array of dorsal ridges. The sequence ends with its flukes breaking above the water in an arching motion and re-entering at about a 45 degree angle. This action initiates the deep-dive phase.

Normally, the whale will remain submerged for an average of from five to eight minutes, but in the lagoon the mean is from three to five minutes. Upon resurfacing after the deep-dive,

the animal repeats the entire respiratory-deep dive sequence. Gray whales will seldom deviate from this respiratory behavioral pattern unless frightened or agitated in some manner.

SOCIAL INTERACTION AREA

From the staging area the whales gradually swam south into the lagoon preferring the shallower waters along the west bank. Very few animals were observed moving down the deeper mid-channel or along the east bank. Depths along the west bank vary from a few feet to less than five fathoms as determined by fathometric readings. Captain Scammon's observations during the late nineteenth century confirm the fact that the gray whale has a penchant for very shallow water and generally will forsake the deeper waters of the lagoon.

The lagoon is not much more than a mile wide for a distance of some 10 miles inland from the entrance. It then broadens off Brushy Island (Isla Broza) (Fig. 2f). Within this broader portion of the lagoon, off the northern tip of Brushy Island, much of the behavior which was interpreted as social orientation and interaction took place (Fig. 2e). Gilmore (1960) has suggested that gray whales are segregated by age, sex, and reproductive condition in various areas of Scammon's Lagoon. His "outer" and "intermediate" areas essentially correspond to my staging and social interaction areas, respectively.

Singly and in pairs and daily from dawn until about 1100, a line of whales moved into this section of the lagoon. Sauer (1963) recorded similar behavior for gray whales within this time frame in Boxer Bay at St. Lawrence Island, Alaska. The whales moved south, generally preferred the western side of the lagoon, crossed gradually towards the east bank, turned, moved north for a mile or two, then crossed again to the west side. This general counterclockwise pattern of movement was also observed by Sauer in Boxer Bay and Fay (1963) at Kangee, along the southern coast of St. Lawrence Island. The overall pattern resembled a convection current (Fig. 2d). Within the area described, the whales deviated from their respiratory-diving cycle; the basic pattern being altered almost completely. They stayed near the surface, respired at irregular intervals, then executed deep-diving procedure with caudal peduncles arched and flukes exposed.

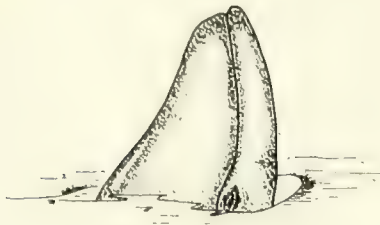


Figure 2. Scammon's Lagoon, Baja California, Mexico: a, entrance; b, staging area; c, the nursery; d, arrows indicate preferred direction of gray whale movement in the social interaction area; e, social interaction area; f, Brushy Island. Depth is indicated in fathoms.

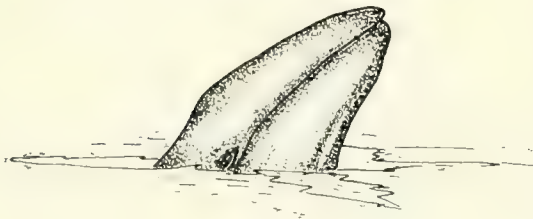
However, rather than staying submerged for four or five minutes, they surfaced again in one or two minutes. Interspersed with these deviations was a constant display of massive, triangular

heads poised erect above the sea's surface. Heads were visible in all directions around the lagoon. At any one time during the hours mentioned no fewer than half-a-dozen gray whale heads

SPYHOPPING POSTURES

MODE 1

TRIANGULAR PROFILE

MODE 2

ARCUATE PROFILE

Figure 3. Spyhopping postures assumed by the gray whale, *Eschrichtius robustus* in Scammon's Lagoon. A parturating female was observed exposing her head as in Mode 2.

could be seen bobbing up in this section of Scammon's Lagoon. This perplexing behavioral trait is called spyhopping (Fig. 3).

Observations indicated that there was a general chronological order coupled with specific behavioral activities. The early morning hours to approximately 1100 included the basic pattern of whales circling within the social interaction area, a great deal of spyhopping and occasional breaching. Whales remained surfaced for prolonged periods of time, blowing slowly and rolling over exposing lateral surfaces and flippers. Females were observed nursing newborn calves.

During these hours the whales were easily approached by small boats propelled by oars. My experiences approaching dolphins of the genera *Globicephala*, *Delphinus*, and *Orcinus* in small boats showed that the high-frequency sound of an outboard motor and the cavitation shock-wave created by the propeller irritated or frightened them. Evasive maneuvers consisted of

erratic course changes after deep-diving and swimming submerged at an increased rate of speed along with prolonged deep-dive periods. From all indications, they appeared to ignore a boat powered by oars or under sail. I have found that grays can often be approached rather closely by larger boats powered by diesel engines which are throttled back. The diesel produces a much lower frequency sound. Although the above is true for adult whales, yearlings or adolescents are difficult to approach in anything but a small boat under oars.

Copulatory behavior.—There was a noticeable change in the attitude and general behavior of the whales beginning in the late morning and lasting until early afternoon, ca. 1100–1300 hrs. During this interval there was an evident hiatus in surface and above-surface activity. The whales became skittish and unapproachable. This anticipatory-phase behavior was manifested by the crown of the head and blow-holes barely breaking water, followed by rapid exhalation and inhalation along with an increase in swimming speed and circling. Gradually, some of the animals began to form trios. This episode was a prelude to actual mating activity during the afternoon and early evening from about 1300 hours to dusk.

The mating triad consists of two males, of which at least one is sexually mature, and an oestrative female. The role of the assisting male or helper bull is not fully understood but he seems to act as a stabilizing agent keeping the copulating pair together in a venter-to-venter attitude (Figs. 4 and 5). Just prior to intromission as well as during copulation there was a great deal of flaying about of caudal peduncles and flukes, rapid rolling and fluke-stands (flukes extended vertically above the lagoon's surface), especially on the part of the assisting male. Mating is a prolonged affair among gray whales, lasting well over an hour in many instances. During the four days spent in Scammon's Lagoon observing gray whale behavior, five confirmed mating sequences were observed. The photographs of the copulating whales (Fig. 4) were taken in the social interaction area off Brushy Island by photographer Bill Philbin. At approximately 1600 hrs. on 30 January 1973, the 13 foot skiff used was unavoidably drawn into a mating interlude by the turbulence generated by the copulating pair and the circling of the helper bull. The mating took place at the surface, in full view, and lasted well over an hour. During

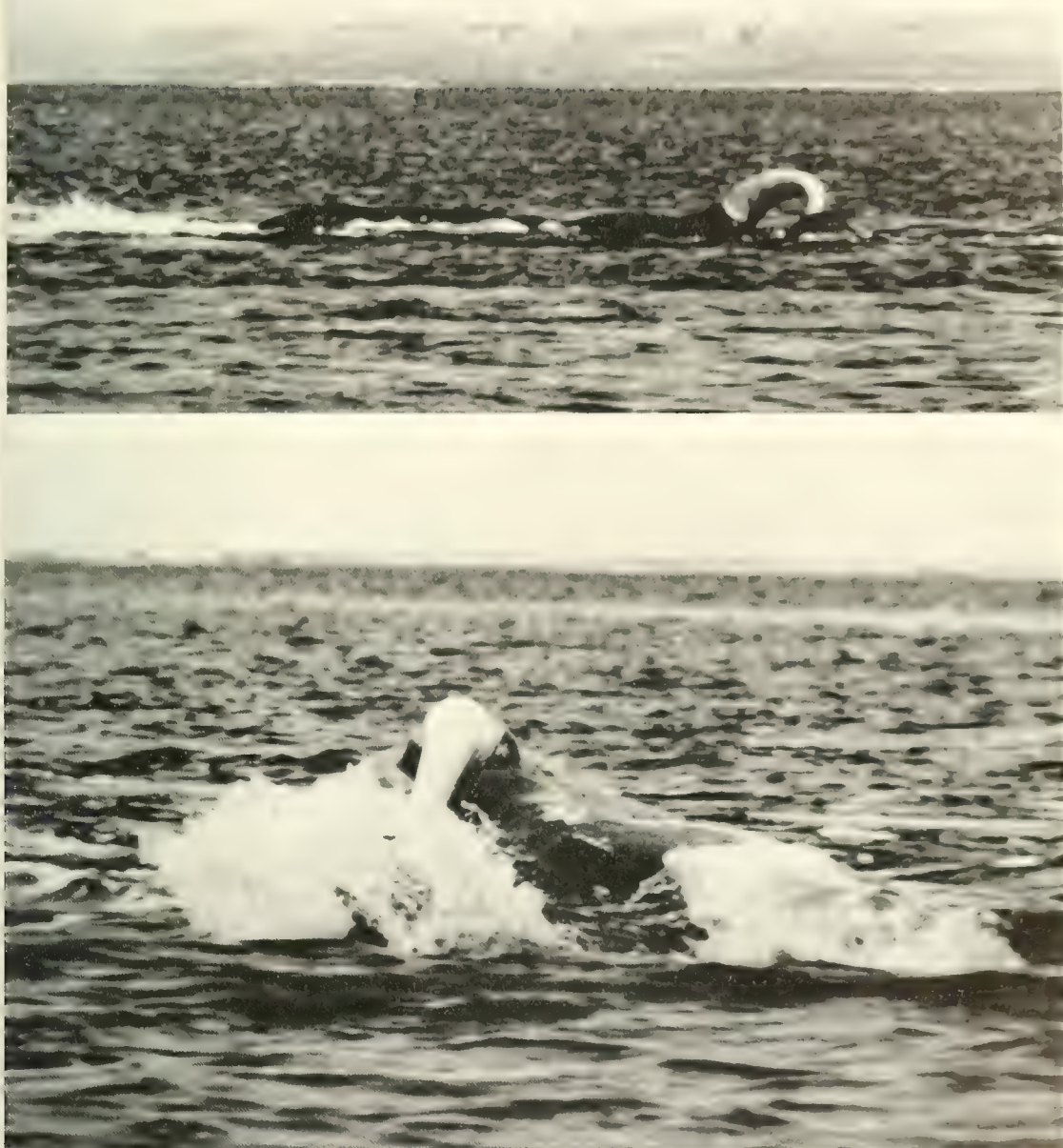


Figure 4. (Top), two copulating gray whales observed in Scammon's Lagoon. Note the everted, cone-shaped vulva of the female. The penis of the male was between 5.5–6 feet in length. (Bottom), the semi-flaccid penis is seen here just as intromission was terminated as the pair rolled with the venter toward the surface and the female submerged. Anterior is to the right in each photograph.

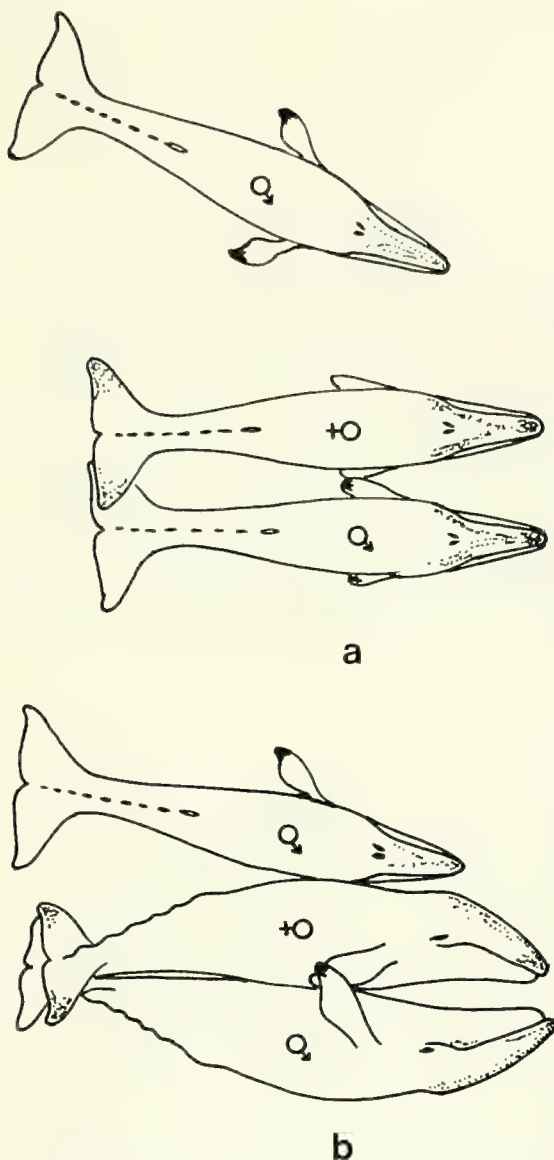


Figure 5. A mating triad of gray whales, *Eschrichtius robustus*: a, dorsal view of the lateral or side-by-side, precopulative swimming posture with the helper bull (top) generally swimming off to one side and somewhat behind the mating pair (bottom); b, dorsal view of the venter-to-venter copulative posture of the mating pair while in a horizontal position with the helper bull in a stabilizing status.

copulation venter-to-venter was the initial posture with flukes aligned and caudal peduncles rigid and extended, forward motion had ceased and the whales were horizontal. On one occasion during our involvement with this mating triad, one of the males (it was impossible to determine

whether it was the mating or helper bull) executed a fluke-stand not more than a meter off our starboard side. This consisted of 15 feet of the caudal peduncle rigidly extended perpendicular to the lagoon's surface with its eight foot wide flukes spread straight out. This position was maintained for at least 10 seconds before the whale submerged beneath the skiff. Fluke-stands like this were frequently sighted in the social interaction area during mating. They have also been observed during mating interludes along the Southern California coast.

Only once during mating sightings in the lagoon was any deviation from the mating-triad pattern observed. Leatherwood and Philbin informed me that they witnessed a full-scale copulation involving only two adult gray whales. A calf with a distinctive brown patch on its right side was seen among the mating animals and on occasion was forced from between the copulating pair. In all probability, the calf was orphaned or abandoned seeking a mother for sustenance. This assumption was reinforced some time later when it was again sighted some distance away from the mating site and alone. Later, the infant became stranded in a shallow inlet on the ebbing tide. Three stranded calves were sighted in the outer portions of Scammon's Lagoon by the end of January.

OBSERVATIONS OF MATING OUTSIDE OF THE LAGOON

On 26 February 1973, I observed a northbound mating trio one mile southeast of Whites Point, Palos Verdes Peninsula. The whales remained surfaced for most of the 45 minutes that we were able to stay with the animals before they became skittish and terminated the episode. No other gray whales were within the vicinity to confuse observations. All three of the animals were large with estimated lengths of 35–40 feet. The mating pair swam side-by-side for approximately 100 yards before abruptly rolling over onto their sides, the male on his right, the female on her left. Intromission was accomplished just below the surface as they merged venter-to-venter. The helper bull slowly swam around and under the copulating pair. Gradually, the mating whales rolled gently away from each other until they were again side-by-side, but with ventral surfaces up and exposed above the sea's surface (Fig. 4). The penis was still inserted in the female's genital

orifice but retracting. At this time, the helper bull swam obliquely in towards the now upside-down pair, turned and came up broadside against the copulating male, nudging him gently over with a firm and deliberate action. The duration of this episode was approximately 10 minutes. I observed this procedure and general sequence three times before the whales deep-dove and ended copulation. In all three instances the same male copulated with the female. Both mating animals were about the same length. Only once during the mating episode was I able to identify which member of the mating pair the helper bull actually assisted.

DISCUSSION

Two distinct modes of vertical, head-above-surface posturing became manifest after many hours of observing spyhopping behavior. The first and most obvious visual-observing posture was the whale's head smoothly rising above the lagoon's surface and presenting a nearly vertical, *triangular profile* (Fig. 3), remaining motionless and vigilant for a number of seconds; and then submerging again, scarcely disturbing the sea's surface. In the second mode, the animal displayed an *arcuate profile* with the head held obliquely to the plane of the lagoon's surface (Fig. 3). The characteristically convex cranium and pronounced protrusion of the distal tip of the rostrum over the terminus of the mandibula is accentuated by the concave-shape of the throat region. The posture of the submerged portion of the body was unobservable.

Because of the consistency in the pattern of spyhopping, it is probable that the gray whales are not only visually orienting themselves within their physical surroundings (Scammon, 1874) but also observing each other. Spyhopping behavior may well serve as a means of sex identification. Physically, the female is somewhat larger than the male (Scammon, 1874; Rice and Wolman, 1971). Walker (1971) maintains that the female has a distinctly narrower cranial profile than the male. Otherwise, there does not appear to be any other external method of discerning between the sexes except for external genital differences. Subtle differences between sexes may be expressed in the mode of posturing during spyhopping. The male may characteristically display his sex by assuming one of the

forementioned spyhopping posture. The distinctive profile and the female, the spyhopping is the single most obvious behavioral feature observed in the social interaction during the morning hours and preceding mating. Spyhopping and mating have been observed along the California coast during both legs of the migration. Spyhopping has been interpreted as orientation behavior involved in migratory navigation (Scammon, 1874); as a method for establishing location and direction from learned reference points, such as prominent headlands (Walker, 1971 and Daugherty, 1972); as a method of feeding whereby gravity is used to aid food to pass down into the digestive tract (Walker, 1971); and, possibly, as a vigilance stance. I believe that spyhopping plays an important role in the social behavior and sexual interaction of the gray whale.

ACKNOWLEDGMENTS

I am grateful to Donald R. Patten and Shelton P. Applegate, both of the Natural History Museum of Los Angeles County, and to John C. Ljubenkov and Robert Osborn of the Cabrillo Marine Museum, San Pedro, California for their constructive comments and editing of the manuscript. I am especially indebted to the American Cetacean Society and the Los Angeles City School District for their support of this research. I also wish to thank William Philbin for allowing me to use his exceptional photographs, and to the many individuals who relayed their observations and information, especially Steve Leatherwood of the Naval Undersea Research and Development Center, San Diego.

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BATS OF MARGARITA ISLAND, VENEZUELA, WITH ZOOGEOGRAPHIC COMMENTS

JAMES DALE SMITH¹ AND HUGH H. GENOWAYS²

ABSTRACT: Sixteen species of bats are reported from Margarita Island, Nueva Esparta, Venezuela. These include two species of emballonurids, one noctilionid, two mormoopids, nine phyllostomatids, one vespertilionid, and one molossid. Accounts including natural history and taxonomic comments are given for each species. The chiropteran fauna of Margarita Island is compared with the bat faunas of the adjacent Venezuelan mainland and islands off the northern coast of South America, including Trinidad and other Antillean islands. It is concluded that the chiropteran fauna of Margarita Island represents an attenuated mainland fauna.

Margarita Island is located approximately 25 kilometers north of the Venezuelan mainland off the Araya Peninsula in northeastern Venezuela. It is the second largest island (approx. 850 square miles) of the Netherland Antilles and comprises the Venezuelan state of Nueva Esparta along with the smaller, adjacent islands of Coche and Cubagua. These three Venezuelan islands are located on the continental shelf and probably were continuous with the mainland during Pleistocene fluctuations in sea level.

Margarita Island actually consists of two islands connected by a narrow isthmus (Fig. 1). Each island has a central mountain mass; Cerro Copey on the eastern island is approximately 957 m in elevation, whereas, Cerro Los Cedros, on the western island reaches 792 m. The majority of the island is covered by a low, xeric thorny scrub forest. A somewhat higher and denser thorny scrub forest of acacia trees and tall cacti occur in the more inland regions. On the eastern slopes of the mountains the vegetation becomes more mesic in character and limited areas of low montane rain forest occur on the tops of the mountains and in the wetter valleys.

Coconut palms and tropical fruit trees are found on the eastern slope of Cerro Copey. This eastern range of mountains apparently has a rainshadow effect and results in the xeric condition of the western portion of the island. Mangrove swamps are widespread on the southeastern coast and are extensive along the isthmus connecting the two land masses. The capital city of Porlamar, located on the eastern coast at the foot of Cerro Copey, is the population center of the island.

Bats were collected and studied in northeastern Venezuela and on Margarita Island by one of us (Smith) from February 1966 to May 1967. Field investigations were supported by the University of Kansas—Universidad de Oriente Project of the Ford Foundation. The authors wish to express their thanks to Nancy Smith, Philip Montgomery, Luis Urosa, and M. Leon for their assistance in collecting and preserving material.

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² The Museum, Texas Tech University, Lubbock, Texas 79409.



Figure 1. Map showing localities mentioned in text: 1, San Francisco de Macanao; 2, Cerro Tragaplata; 3, La Estancia; 4, Paraguachí; 5, Salamanca; 6, Cerro Matasiete; 7, La Asunción; 8, Guatamare; 9, La Aguada; 10, Hacienda Ochenta; 11, El Vallé; 12, Porlamar; 13, Laguna Marites. The 200 meter contours also are indicated.

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are deposited in the Museum of Natural History, The University of Kansas, unless otherwise noted.

All measurements employed in this study are defined by Smith (1972:6) and were taken with dial calipers, calibrated in twentieths of a millimeter and were recorded to the nearest tenth of a millimeter. Measurements of embryos are given as crown-rump lengths.

ACCOUNTS OF SPECIES

FAMILY EMBALLONURIDAE

Pteropteryx macrotis trinitatus Miller, 1899

Specimens examined (24).—Cave SW El Vallé [Musso (1962:167) indicates this cave is surely Cueva del Piache], 1 (MCZ); no specific locality, 23 (RMNH).

Additional records.—Guatamare, near El Vallé (Hummelinck, 1940:69); Cave near La Asunción, Carretera a Porlamar; Cueva Chaure, Cerro Atagua (Musso, 1962:166).

This species apparently is one of the more common bats in the mesic regions of Margarita Island. All of the individuals reported by Musso (1962:166) were found in caves. In a cave near La Asunción, he encountered *Saccopteryx leptura* living with a large colony of *P. m. trinitatus*.

Measurements of the material examined by

TABLE 1. Selected cranial and external measurements of *Noctilio leporinus* from the Antilles and northeastern South America. Superscript numbers indicate a sample size that differs from those given in left-hand columns.

Number and sex	Forearm	Greatest length of skull	Condylar-basal length	Zygomatic breadth	Mastoid breadth	Length of maxillary toothrow	Length of mandible
<i>Noctilio leporinus mastivus</i> , Puerto Rico (Anthony, 1925:16-17)							
5 ♂	86.7 ⁷	27.3	—	20.3	19.6	—	19.1
	(85.0-88.0)	(26.6-28.5)	—	(19.8-20.7)	(18.0-20.7)	—	(18.5-19.4)
5 ♀	83.9 ⁷	25.5	—	18.9	17.2	—	18.0
	(80.0-85.8)	(24.9-26.3)	—	(18.6-19.1)	(16.8-17.8)	—	(17.7-18.4)
<i>Noctilio leporinus mastivus</i> , Dominica, Lesser Antilles							
1 ♂	88.9	25.6	24.9	20.0	18.5	10.6	18.6
3 ♀	87.9	24.8	23.8	19.3	17.0	10.0	17.6
	(86.4-88.7)	(24.6-24.9)	(23.6-23.9)	(19.1-19.5)	(16.9-17.2)	(10.0-10.1)	(17.5-17.7)
<i>Noctilio leporinus mastivus</i> , Trinidad*							
4 ♂	85.6	27.4 ³	24.7 ¹	19.6	19.0 ¹	10.5	18.7 ¹
	(82.7-88.0)	(26.7-28.5)	—	(18.7-20.2)	—	(10.0-10.8)	—
3 ♀	86.1 ⁷	24.8, 26.9 ²	23.5, 24.6 ²	19.4	16.9, 17.0 ²	10.4	17.4, 17.7 ²
	(82.9-89.7)	—	—	(19.3-19.5)	—	(10.1-10.7)	—
<i>Noctilio leporinus mastivus</i> , Margarita Island, Venezuela							
1 ♀	85.8	24.1	23.5	18.5	17.5	10.0	17.3
<i>Noctilio leporinus mastivus</i> , Estado Sucre, Venezuela							
1 ♂	87.9	26.3	24.9	20.1	19.9	10.8	18.6
5 ♀	87.2	25.2	24.0	19.0	17.0	10.3	17.7
	(84.1-92.1)	(24.8-25.7)	(23.5-24.4)	(18.7-19.4)	(16.3-17.8)	(10.1-10.5)	(17.6-17.8)
<i>Noctilio leporinus leporinus</i> , Surinam (Husson, 1962:68)							
5 ♂	79.0	25.0	23.3	18.4	16.8 ³	10.4	17.8
	(77.3-81.2)	(23.3-26.2)	(22.8-23.7)	(17.0-19.1)	(14.9-18.4)	(10.3-10.5)	(17.4-18.3)
6 ♀	78.8	24.5 ⁵	22.6	17.8	15.7 ⁵	10.0	17.3
	(78.5-82.1)	(24.1-24.9)	(22.0-23.2)	(16.8-18.3)	(15.1-16.0)	(9.1-10.2)	(17.1-17.6)

* Includes measurements of two males and one female from Goodwin and Greenhall (1961:219).

us and those published by Musso (1962) agree with those given by Goodwin and Greenhall (1961:216) for four specimens of *P. m. trinitatus* (including the holotype) from Trinidad.

Saccopteryx leptura (Schreber, 1774)

Specimens examined.—None.

Additional records.—Hacienda Ochenta; Cueva near La Asunción, Carretera a Porlamar (Musso, 1962:167); El Vallé (Pirlot and León, 1965:369).

Pirlot and León (1965:369) reported this species as very abundant in the forest, on the higher hills of the eastern portion of the island. Individuals were found in groups of two to five living in holes in rocks and fallen trees, and between the buttresses of *Ceiba pentandra*. Musso (1962:167) found this species roosting with a large colony of *Peropteryx macrotis trinitatus* in a cave near La Asunción.

FAMILY NOCTILIONIDAE

Noctilio leporinus mastivus (Vahl, 1797)

Specimens examined (1).—1½ km N San Francisco de Macanao, 75 m, 1.

A nonpregnant, lactating female, represents the first record of this large fish-eating species from Margarita Island. It was captured at dusk in a mist-net set across a small arroyo which drained into a small artificial pond. Lesser nighthawks, *Chordeiles acutipennis*, were captured at this time as they foraged over the pond. The vegetation around the pond was low, thorny scrub.

Koopman (1968:2) discussed the subspecific status of *Noctilio leporinus* with particular reference to *N. l. mastivus*, and Davis (1973) has recently reviewed the species *leporinus*. The selected external and cranial measurements given

in table 1 clearly show that the Antillean bats are much larger in size than those from Surinam, which is the type locality of *N. l. leporinus* as restricted by Thomas, 1911:131. Both Koopman (1968) and Davis (1973) proposed that the antillean population should be referred to the race *N. l. mastivus*. In comparing cranial and external measurements of our specimen from Margarita Island and several from the adjacent mainland, we found them to agree more closely in size with the Antillean bats than those from Surinam. Therefore, we concur with Davis (1973) in applying the name *N. l. mastivus* to the populations of large fish-eating bats from northeastern Venezuela.

Specimens used for comparison are as follows. —BRAZIL: Cruzeiro do Sur, Acre, 1 (LACM). CUBA: Km. 7, between San Juan de Las Lajas and La Ruda, Habana, 2 (TCWC). DOMINICA: Clarke Hall Estate, 100 ft, St. Joseph Parish, 1 (KU); Mouth of Layou River, sea level, St. Joseph Parish, 3 (KU); no specific locality, 2 (1 BMNH, 1 USNM). TRINIDAD: Fyzabad, 4 (3 KU, 1 TCWC); Peral, 4 (TCWC). VENEZUELA: 1½ km NW El Pilar, Sucre, 6 (KU).

FAMILY MORMOOPIDAE

Pteronotus parnellii fuscus J. A. Allen, 1911

Specimens examined (31).—Cueva Atagua, Cerro Atagua, 5 (MLS); Cerro Matasiete, 2 km N, 2 km E La Asunción, 305 m, 1 (USNM); El Vallé, 50 m, 2; Cueva Honda del Piache, SE El Vallé, 2 (RMNH); La Aguada, 3 km S La Asunción, 53 m, 12 (USNM); Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 9.

Parnell's mustached bat appears to be rather common on Margarita Island. The ecological limits of this species are not well known. It was encountered in both xeric and mesic habitats on the island.

At Cueva El Convento, near San Francisco de Macanao, *P. p. fuscus* was collected in close association with *Leptonycteris curasoae*. It is not known whether individuals of *P. parnellii* were roosting singly or as a segregated cluster within the colony of *Leptonycteris* as both species were obtained with a single discharge of a shotgun. The bats were roosting in a dome-like depression in the ceiling, about ten feet above the floor of the dry, guano-filled cave. One wall of the roosting chamber was open to the outside by

way of a vertical passageway and the room was dimly lighted. The presence of guano indicated a long and continuous use of the cave by bats. Two mandibles of *P. parnellii* were found among the skeletal remains of weathered owl pellets removed from the floor.

One female, captured on 16 July, was pregnant with one embryo that measured 27. Two females taken on 12 November, showed no signs of reproductive activity.

In analyzing the geographic variation of *P. parnellii*, Smith (1972:77) assigned specimens from Margarita Island and the Caribbean versant of Venezuela to the subspecies *P. p. fuscus*. Although individuals of *P. parnellii* from Margarita fall well within the range of variation of mainland populations of *P. p. fuscus*, they show a slight reduction in overall size. Populations of *P. p. rubiginosus* from the Amazon Basin are considerably larger in cranial and external size (Smith, 1972). Specimens of *parnellii* from Trinidad appear to more closely resemble *P. p. rubiginosus* than *P. p. fuscus*.

Mormoops megalophylla tumidiceps Miller, 1902

Specimens examined (4).—Cueva Honda del Piache, SE El Vallé, 3 (RMNH); Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 1.

Additional record.—El Vallé (Pirlot and León, 1965:369).

The ghost-faced bat does not appear to be an abundant species on Margarita Island and is common only locally on the Venezuelan mainland. One of our specimens is a right mandible found in the owl pellet material from Cueva El Convento. The geographic variation of this species is discussed by Smith (1972).

Selected external and cranial measurements of two males from Cueva Honda del Piache are as follows: length of forearm, 55.6, 55.2; condylobasal length, 14.4, 14.1; zygomatic breadth, 9.8, 9.6; rostral breadth, 5.5, 5.4; length of maxillary toothrow, 8.1, 7.8.

FAMILY PHYLLOSTOMATIDAE

Micronycteris megalotis megalotis Gray, 1842

Specimens examined (3).—El Vallé, 2 (MCZ); Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 1.

Additional records.—all from Museo (1962:168).

Cerro Tragaplata; La Estancia, 2 km W Paraguachi; Salamanca; San Francisco de Macanao.

According to Musso (1962:168), this species is widely distributed on the island. Selected external and cranial measurements of one male and one female, respectively, from El Vallé are as follows: length of forearm, 32.8, 33.7; zygomatic breadth, 8.7, 8.6; rostral breadth, 4.8, 4.8; length of maxillary toothrow, 6.7, 6.9; condylobasal length, —, 15.7. These measurements agree with those given by Sanborn (1949) and Husson (1962) for the subspecies *M. m. megalotis*. At Cueva El Convento, this species was represented by a right lower jaw found in the weathered remains of owl pellets.

Phyllostomus discolor discolor Wagner, 1843

Specimens examined (6).—El Vallé, 50 m, 6.

Pirlot and León (1965:369), first reported this bat on Margarita Island. Their material also was from El Vallé, the only locality on the island from which this species has been recorded. The ecological preferences of *P. discolor* seem to be for mesic habitats and for this reason the species may be restricted to the northeastern portion of the island.

Of five females mist-netted on July 15 and 16, one contained one embryo measuring 17. Two others were not pregnant but were lactating. A male taken at the same time had testes measuring 5 mm in length. These bats were captured as they foraged in a peach and mango grove.

Valdez (1970), after studying the geographic variation of *Phyllostomus discolor*, employed the name *P. d. discolor* for populations east of the Andes. Power and Tamsitt (1973) have questioned the validity of the recognition of intra-specific names in this species. In the absence of an extensive study of geographic variation in northern South America, we have assigned our material to *P. d. discolor*.

Selected external and cranial measurements of the four females (average with extremes in parentheses) and two males, respectively, from El Vallé are as follows: length of forearm, 61.3 (60.1–62.2), 62.0, 63.3; condylobasal length, 26.4 (25.3–26.6), 25.8, 26.9; zygomatic breadth, 15.4 (15.0–16.0), 15.4, 15.6. These measurements agree with those given by Sanborn (1936:98) for specimens from Brazil, Venezuela, and French

Guiana, and by Goodwin and Greenhall (1961:238) for material from Trinidad.

Glossophaga longirostris longirostris Miller, 1898

Specimens examined (26).—El Vallé, 50 m, 24 (3 MCZ); 1½ km N San Francisco de Macanao, 75 m, 2.

Additional records.—La Estancia, 2 km W Paraguachi; Salamanca; Cueva del Piache; Hacienda Ochenta; San Francisco de Macanao (Musso, 1962:169); El Vallé (Pirlot and León, 1965:369).

G. M. Allen (1902:96) reported on three specimens from a large cave near El Vallé which he referred to the species *Glossophaga soricina*. One was an adult male, another a young (sex unknown) individual with deciduous teeth, and the third specimen was an adult female. He noted that the latter seemed distinct from the other two and thought that it might represent an undescribed species. We have examined Allen's three specimens and found that only the female is an adult. We concur with Koopman (1958:437) who assigned all three bats to *Glossophaga longirostris*.

Pirlot and León (1965:369) report two male *G. soricina* from El Vallé. We have not examined these specimens, but suspect that these, too, are but immature individuals of *G. longirostris*. Adult *G. longirostris* are easily distinguished from *G. soricina* on the basis of greater length of forearm. In addition, the upper incisors of *longirostris* are nearly equal in size and are equally procumbent. The outer incisors of *soricina* are smaller than the inner pair and somewhat less procumbent.

Eight of fourteen females mist-netted in a peach and mango grove at El Vallé on 15 July, carried one embryo which averaged 17.0 (12.0–20.0) crown-rump length. The remaining six females showed no sign of reproductive activity.

Table 2 shows the means and extremes of several selected external and cranial measurements of *G. longirostris* from selected localities. Our material from Margarita Island is well within the range of variation of the mainland *G. l. longirostris*. These measurements also widely overlap those given for the Antillean race *G. l. rostrata*. Whether or not this indicates a close relationship between these populations is not clear at this time. However, this may indicate that the source for the Antillean populations may have been directly from the mainland rather than from the mainland by way of Trinidad and Tobago. Until

TABLE 2. Selected cranial and external measurements of *Glossophaga longirostris* from the Antillean eastern South America. Superscript numbers indicate a sample size that differs from those given in the left-hand column

Number	Forearm	Condylobasal length	Breadth of braincase	Mastoid breadth	Breadth of rostrum at canines	Length of maxillary toothrow
<i>Glossophaga longirostris elongata</i> , Curacao (Miller, 1913:429)						
20	37.3 (35.6–39.0)	22.5 (21.8–23.2)	8.7 (8.4–9.0)	—	—	8.1 (8.0–8.4)
<i>Glossophaga longirostris longirostris</i> , Margarita Island, Venezuela						
9	37.8 (36.4–29.6)	21.2 (21.0–21.6)	8.8 (8.5–8.9)	9.2 (8.8–9.5)	4.0 (3.7–4.3)	7.9 (7.7–8.2)
<i>Glossophaga longirostris longirostris</i> , Estados Sucre, Venezuela						
12	37.4 (36.2–39.4)	21.2 (20.4–22.0)	8.8 (8.5–8.9)	9.4 (9.1–9.6)	4.1 (3.9–4.2)	7.8 (7.5–8.0)
<i>Glossophaga longirostris longirostris</i> , La Guaira, Venezuela (Miller, 1913:429)						
10	37.2 (35.4–38.6)	21.7 (21.0–22.4)	9.1 (8.8–9.4)	—	—	8.1 ^o (7.8–8.8)
<i>Glossophaga longirostris major</i> , Trinidad						
5	40.2 ^o (39.8–41.0)	21.5 (20.8–22.2)	10.1 ⁴ (10.0–10.3)	9.1 ^o (9.0–9.2)	4.2 (4.1–4.3)	8.1 (7.9–8.4)
<i>Glossophaga longirostris rostrata</i> , Grenada						
9	37.7 (37.1–38.5)	21.5 (20.8–22.0)	8.8 (8.6–9.0)	9.4 (9.2–9.7)	4.1 (3.8–4.4)	7.9 (7.8–8.0)
<i>Glossophaga longirostris rostrata</i> , St. Vincent						
10	37.4 (36.4–38.8)	21.1 (20.6–21.9)	—	9.4 (9.3–9.6)	4.0 (3.9–4.2)	7.7 (7.5–7.9)

this relationship is better understood we tentatively assign our material to *G. l. longirostris*.

Leptonycteris curasoae Miller, 1900

Specimens examined (88).—El Vallé, 50 m, 5; Cueva El Convento, 1 km N, 1 km W San Francisco de Macanao, 100 m, 81; 1½ km N San Francisco de Macanao, 75 m, 2.

Additional record.—The holotype and type series of *L. c. tarlosti* from El Vallé (Pirlot, 1965:6–7).

Individuals of this apparently widespread and common species were captured in mist-nets and shot in caves. The majority of our material resulted from two visits (July and November) to Cueva El Convento, near San Francisco de Macanao. The cave is described in the account of *Pteronotus parnellii fuscus*, a species found living in direct association with this colony of *Leptonycteris*.

When first discovered in July the colony was composed of approximately 4000 females nursing nearly full-grown young. The young bats had

unfused phalangeal epiphyses and were covered with sparse greyish, juvenile pelage. In addition, these young were in varying stages of losing the upper deciduous canines and lower incisors, the third upper molars and the permanent lower incisors were nearly completely erupted, and all cranial sutures were unfused. The forearms of 15 young bats averaged 53.3 (52.0–55.2) in comparison with 53.4 (51.3–55.8) of 61 adult females. No adult males were captured on the July visit.

In November, the composition of the colony had changed. There were no young individuals with unfused wing bones, and adult males in breeding condition (testes 6–8 mm in length) were present. Of the 34 females captured in November seven were pregnant; each with one small embryo which averaged 6.3 (3.1–11.3). The smallest embryos had the limb buds only slightly differentiated, whereas these structures were relatively well developed in the largest embryos. Skeletal elements and complete skulls

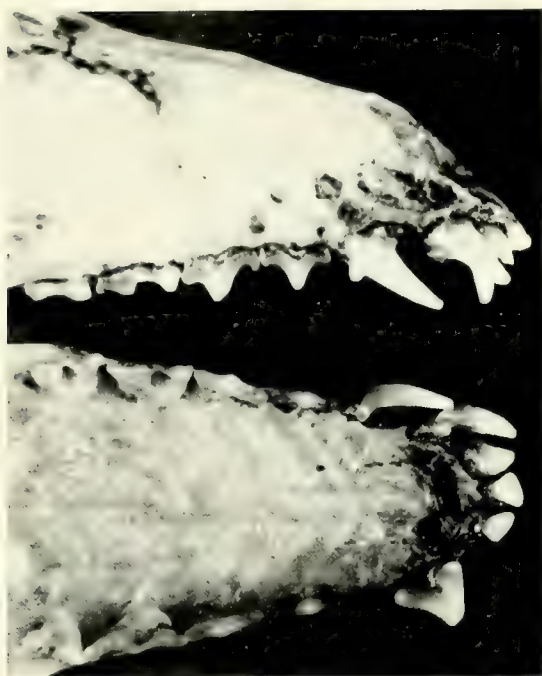


Figure 2. Top, right lateral view of the rostrum of an adult female *Leptonycteris curasoae* (KU 118206) showing the hyperdontia of the canine. Bottom, occlusal view of same.

of *Leptonycteris* also were encountered in the owl-pellet material from the floor of the cave.

Hyperdontia in the genus *Leptonycteris* was encountered only in the species *L. sanborni* by Phillips (1971:76). In our series of *L. curasoae* from Margarita Island, we found one adult

female (KU 118206) with a unilateral duplication of the upper right canine (Fig. 2). Another adult female (KU 118193) exhibited a persistent left upper deciduous canine in the space between the permanent canine and first premolar; all teeth were fully erupted and partially worn. Our sample also indicates that incisors are apparently lost frequently during life. In two individuals upper premolars had been lost and in another the second right upper molar was lost.

Pirlot (1965:607) evidently was unable to compare his material from Margarita Island with specimens from Aruba, Curacao, or Bonaire when he described *L. c. tarlosti*. Table 3 shows selected external and cranial measurements (average with extremes in parentheses) of specimens of *L. curasoae* from Margarita, Aruba, Curacao, and Bonaire islands. As can be seen, there is a great deal of overlap, especially between individuals from Margarita and Aruba. Although individuals from the oceanic islands Curacao and Bonaire appear to have somewhat narrower crania, a meaningful interpretation of any geographic trend is difficult with so few specimens. There appears to be little evidence to support the recognition of the population from Margarita Island as a distinct race. The species is widespread along the coastal lowlands of northern Colombia and Venezuela (Marinkelle and Cadena, 1972:53; Matson and Brown, 1974) and we believe that an analysis of geographic variation will show that mainland and insular populations are undifferentiated. We therefore consider *Leptonycteris curasoae* to be monotypic.

TABLE 3. Selected cranial and external measurements of *Leptonycteris curasoae*. Superscript numbers indicate a sample size that differs from those given in the left-hand column.

Number	Length of Forearm	Zygomatic breadth	Breadth of braincase	Breadth across canines	Length of maxillary toothrow	Condylor-basal length	Length mandibular toothrow
Margarita Island, Venezuela							
12	53.4 (51.3-55.2)	11.1 ¹¹ (10.7-11.4)	10.1 ¹¹ (9.9-10.4)	4.9 ¹¹ (4.8-5.0)	9.4 (9.0-9.7)	26.4 (25.4-26.9)	10.2 (9.9-10.6)
Aruba Island							
2	54.4 ⁵ (53.7-54.7)	11.4, 11.6	10.2, 10.5	5.1, 5.1	9.6, 9.7	27.0, 27.6	10.7, 10.6
Curacao Island							
5	54.3 (51.4-55.7)	10.9 ³ (10.7-11.3)	10.1 ⁴ (9.8-10.2)	4.9 (4.5-5.1)	9.4 (9.2-9.6)	26.6 ⁴ (26.0-27.2)	10.4 (10.2-10.8)
Bonaire Island							
1	52.5	—	10.2	5.1	9.5	26.8	10.6

TABLE 4. Selected external and cranial measurements of *Artibeus planirostris* from northeast Venezuela and Trinidad. Superscript numbers indicate a sample size that differs from those given in the left hand column.

Number	Forearm	Condylobasal length	Zygomatic breadth	Mastoid breadth	Breadth of rostrum at canines	Length of maxillary tooth
El Vallé, Nueva Esparta, Venezuela						
5	55.9 (52.6-57.4)	24.0 (23.7-24.4)	16.6 (16.2-17.0)	14.7 (14.4-14.9)	7.3 (7.1-7.6)	9.7 (9.4-10.0)
Cumaná, Sucre, Venezuela						
22	58.6 (55.7-61.0)	24.2 (23.7-25.1)	17.2 ²¹ (16.4-17.9)	15.2 (14.8-15.6)	7.6 (7.2-8.2)	9.7 (9.4-10.1)
5 km E San Antonio del Golfo, Sucre, Venezuela						
17	59.6 (56.3-62.9)	24.6 (23.8-25.4)	17.4 (16.6-18.1)	15.2 (14.6-15.8)	7.8 (7.5-8.1)	10.5 (9.6-10.3)
1.5 km NW El Pilar, Sucre, Venezuela						
22	59.8 ¹² (57.1-62.9)	24.6 (24.0-25.4)	17.4 (16.7-18.2)	15.2 (14.6-15.7)	7.9 (7.4-8.5)	10.0 (9.7-10.5)
Various localities on Trinidad						
8	57.1 ⁵ (54.8-58.9)	24.3 ⁷ (23.6-25.1)	17.2 (16.7-17.9)	14.8 ⁷ (14.4-15.6)	7.7 (7.5-7.9)	9.9 ⁹ (9.6-10.2)

Carollia perspicillata perspicillata
(Linnaeus, 1758)

Specimens examined (2).—Las Piedras, 2.

Additional records.—La Estancia, 2 km W Paragachi (Musso, 1962:170).

Two males were captured in a mist-net as they foraged along a dry arroyo bordered by tall broad-leaved gallery forest composed primarily of the fig tree, *Ficus yoponensis*. Musso (1962:170) collected this species from under the roof of an old abandoned house. Only two other species of bats, *Artibeus planirostris* and *A. lituratus*, were netted at this locality.

The forearms of the two males captured 15 July measured 42.2 and 40.5. We follow Goodwin and Greenhall (1961), Husson (1962), and Pine (1972) in assigning our specimens to *Carollia perspicillata perspicillata*.

Artibeus planirostris trinitatis Andersen, 1906

Specimens examined (18).—Las Piedras, 8; El Vallé, 50 m, 10.

Additional records.—Hacienda Ochenta (Musso, 1962:170); El Vallé (Pirlot and León, 1965:369).

This bat is one of the most common species in the wetter portions of the island and the adjacent mainland. At Las Piedras, the fruits of the native fig (*Ficus yoponensis*) were found

in the nets along with both *Artibeus planirostris* and *A. lituratus*. Some flying individuals also were observed carrying a single fruit of this fig.

Two of five females caught at Las Piedras on 15 July each carried one embryo measuring 22.3 and 28.8, respectively. Two other females were lactating and a third showed no signs of reproductivity. In addition, two females collected at El Vallé on 15 July were pregnant with embryos that measured 27 and 28.

We follow Patten (1974) in applying the specific name *planirostris* to these specimens of *Artibeus* from Margarita. Although our material of this species from Margarita averages slightly smaller in external and cranial size than specimens from the adjacent Venezuelan mainland and Trinidad (Table 4), we do not feel justified in recognizing this population as a distinct geographic race. We therefore assign our material to *Artibeus planirostris trinitatis*.

Artibeus lituratus palmarum

J. A. Allen and Chapman, 1897

Specimens examined (6).—Las Piedras, 1; El Vallé, 50 m, 5.

Additional records.—Salamanca (Musso, 1962:170); El Vallé (Pirlot and León, 1965:369).

This large *Artibeus* does not appear to be common on Margarita Island. Musso (1962) first

reported the species on the island on the basis of one adult male. Pirlot and León (1965) reported 17 specimens of *lituratus* in their collection from Margarita. One of our specimens was captured in a mist-net set across a dry boulder-filled arroyo bordered by fig trees. *Artibeus planirostris* also was captured at this site. At El Vallé, *A. lituratus* was netted in a peach, mango, and coconut grove. External and cranial measurements of our material agree with those given by Goodwin and Greenhall (1961:261) for specimens from Trinidad.

One of two females captured on 15 July at El Vallé carried a single embryo measuring 25. The testes of three males obtained the same night at El Vallé measured 5, 6, and 7.

Desmodus rotundus rotundus
(E. Geoffroy-St. Hilaire, 1810)

Specimens examined (1).—1½ km N San Francisco de Macanao, 75 m, 1.

Additional records.—El Vallé (Pirlot and León, 1965:360).

Although this species is abundant on the Venezuelan mainland, its presence on Margarita Island was not reported until relatively recently by Pirlot and León (1965). Our specimen, an adult male, was caught in a mist-net set over a dry wash. The specimens reported by Pirlot and León (1965) were captured in a peach, mango, and coconut grove near El Vallé.

In July 1966, the Food and Agriculture Organization of the United Nations reported several cases of paralytic rabies in cattle from the areas of San Antonio and "Ochenta." Cave fumigation was employed by the Venezuelan Ministerio de Agricultura e Cria in an effort to eradicate bats on the island early in 1967.

Selected external and cranial measurements of the individual from near San Francisco de Macanao followed by those (average with extremes in parentheses) of four males from the adjacent mainland (Cumaná and vicinity) are as follows: length of forearm, 59.1, 55.4 (54.1–57.6); condylobasal length, 19.9, 20.4 (20.0–20.7); zygomatic breadth, 11.6, 11.6 (11.2–12.0); length of maxillary tooththrow, 3.3, 3.3 (3.2–3.5). These measurements agree with those given by Goodwin and Greenhall (1961) and Husson (1962) for the nominal subspecies *rotundus*.

Diaemus youngi youngi (Jentink, 1893)

Specimen examined (1).—El Vallé, 50 m, 1.

Additional records.—Sierra del Copey; Cueva del Piache (Musso, 1962:171); El Vallé (Pirlot and León, 1965:6).

The avian vampire was first reported from Margarita Island by Musso (1962:171). In the region around Cerro Copey, Musso noted that *Diaemus* was common throughout the forest and that flying individuals were easily identified by their large white wing tips [*A. planirostris* and *A. lituratus* also possess white wing tips]. Seven individuals of *D. youngi* reported by Musso were from a large colony which he encountered in a hollow tree trunk.

Goodwin and Greenhall (1961:271) described the peculiar oral glands of *Diaemus* which are located in the corners of the mouth. These glands were observed on the specimen from Margarita as well as several individuals from the adjacent mainland. When disturbed, the bat opens its mouth and the two glands evert, nearly filling the oral cavity. Each gland is bulbous in shape and measures about 2–3 mm in diameter when fully everted. The mouth glands of our July-taken specimen appeared to be quiescent because the odor described by Goodwin and Greenhall (1961:271) was not noted. Several February-taken males from the mainland had very active glands that squirted a fine stream of liquid, which had a "mustelid-like" odor, when these individuals were disturbed.

Selected external and cranial measurements of our specimen from Margarita Island, those of three males (average with extremes in parentheses) and one female from the adjacent mainland, and the holotype of *D. youngi* (taken from Husson, 1962:199) are respectively: length of forearm, 52.2, 52.1 (51.1–53.3), 52.3, 50.9; condylobasal length, 21.3, 21.4 (21.2–21.8), 21.4, 21.1; zygomatic breadth, 13.9, 14.0 (13.9–14.1), 13.3, 13.3; breadth of the braincase, 12.5, 13.0 (12.9–13.1), 12.9, 13.0; length of maxillary tooththrow, 3.2, 3.6 (3.5–3.6), 3.5, 3.0. Thomas (1928:288–289) proposed the recognition of a separate race, *D. y. cypselinus*, from Pebas, Perú, based on one female specimen. Later, Sanborn (1949:282–283) reported an additional specimen identified as *cypselinus* from Yarinacocha, Perú. Comparison of the above-listed measurements with those given by Thomas (1928) and Sanborn (1949) suggests to us that the Peruvian subspecies is only slightly larger than *youngi*. In view of the paucity of material, we tentatively retain the name *D. y. cypselinus* as a weakly defined

race. The specimens from northeastern Venezuela and Margarita Island are referred to *Diaemus youngi youngi*.

Other Venezuelan specimens of *Diaemus* that we examined in this study include: Tacal, 11 km SSW Cumaná, Sucre (KU) 1; Chara Santa Rita, 3 km SE Cumaná, Sucre (KU) 1; 2 km S Cachipo, Monagas (KU) 2.

FAMILY VESPERTILIONIDAE

Rhogeessa minutilla Miller, 1897

Specimens examined (2).—El Vallé, 1 (USNM); unspecified locality, 1 (USNM).

Additional record.—Laguna de las Marites (Musso, 1962:171).

The three specimens listed above are the only examples of *Rhogeessa minutilla* from Margarita Island, the type locality. The individual reported by Musso (1962:171) was captured in a mangrove swamp.

Miller (1897:139) described the first specimen from the island as a full species, which it remained until Goodwin (1958:7) relegated it a subspecies of *R. parvula*. Along with the material from Margarita Island, Goodwin assigned specimens from Trinidad, northern Venezuela, and eastern Colombia to this race. LaVal (1973) has recognized *Rhogeessa minutilla* as a distinct species and assigned to it specimens from Margarita Island, northwestern Venezuela, and adjacent Colombia. Tentatively, we follow LaVal's arrangement with some reservations. We believe that when the relationships of these bats in northern South America are fully understood, *minutilla* will prove to be, at most, a geographic race of *R. tumida*.

FAMILY MOLOSSIDAE

Molossus molossus molossus (Pallas, 1766)

Specimens examined (2).—El Vallé, 2 (MCZ).

Additional records.—Guatamare, near El Vallé (Hummelinck, 1940:72); Juan Griego Salamanca (Musso, 1962:172).

This species is probably much more common than available specimens indicate. Musso (1962:172) reported collecting his material (all males) from a bell tower of a church. One of us (Smith) observed this species at dusk as they emerged from under the eaves or out of the rain spouts of houses in Porlamar.

We follow Husson (1962:251) in assigning the specific name *molossus* to our specimens. This species which were reported earlier by Hummelinck (1902:91) under the name *obscura*. Hummelinck (1940:72) and Musso (1962:172) reported their specimens under the species *major*. Examination of material from the Lesser Antilles, mainland South America, Central America, and México leads us to believe that enough inter-population variation exists to warrant the use of the trinomial at this time, although the species is still badly in need of a thorough review.

The specimens from Margarita Island closely resemble typical material of *M. m. molossus* from St. Lucia, Grenada, St. Vincent (all in MCZ), Trinidad (TTU), and a large series from Dominica (KU). Also material from adjacent parts of the mainland (Jusepin, Monagas, and San Antonio del Golfo, Sucre) seem to be assignable to this subspecies (Table 5). A series of specimens from Maripa, Bolívar, are somewhat smaller in size than typical *molossus* but this may be simply a result of local variation (Jones, Smith, and Turner, 1971:23–24). Further delineation of the range of *M. m. molossus* on the mainland and the relationship of the Maripa specimens will have to wait until more material is available; however, it is sufficient at present to say that *M. m. molossus* occurs on the mainland of northeastern South America.

ZOOGEOGRAPHIC COMMENTS

Koopman (1958) has discussed the zoogeography and distribution of bats on islands off the northern coast of South America. We take this opportunity to update Koopman's data based on recent publications and re-examine his conclusions in light of this new information. The islands in the following list are those considered by Koopman (the first number, in parentheses, represents species reported by Koopman, 1958; the second number refers to species presently known from the island followed by the references upon which this number is based): Aruba, (3) 4 (Husson, 1960); Curacao, (6) 8 (Husson, 1960); Bonaire (3) 6 (Husson, 1960); Margarita, (7) 16 (this paper); Trinidad, (44) 63 (Goodwin and Greenhall, 1961, 1962, 1964; Genoways, Baker, and Loregnard, 1973); Tobago, (16) 17 (Goodwin and Greenhall, 1961); Grenada, (11) 12 (Jones and Phillips, 1970). We estimate the bat fauna of northern Venezuela

TABLE 5. Selected external and cranial measurements of *Molossus molossus* from the Antilles and north-eastern South America. Superscript numbers indicate a sample size that differs from those given in the left-hand column.

Number and sex	Forearm	Zygomatic breadth	Breadth of braincase	Condyl-basal length	Length of maxillary toothrow	Breadth of rostrum at canines
Dominica						
7 ♂	38.3 (37.2-39.2)	10.5 ⁶ (10.3-10.9)	8.5 ⁶ (8.4-8.7)	14.8 (14.5-15.3)	5.9 (5.7-6.0)	4.3 (4.1-4.4)
8 ♀	37.8 (36.2-39.0)	10.0 (9.8-10.1)	8.3 (8.0-8.6)	14.1 (13.8-14.6)	5.6 (5.5-5.7)	4.0 (3.9-4.1)
St. Vincent						
1 ♂ (?)	—	10.2	8.7	14.6	5.7	4.2
2 ♀ (?)	—	9.8, 9.9	8.8, —	13.8, 14.4	5.5, 5.7	4.0, 4.0
Grenada						
2 ♀	—	9.7, 10.2	8.3, 8.6	13.7, 14.3	5.2, 5.7	3.8, 4.1
Trinidad						
10 ♂	38.1 (37.0-39.2)	10.8 (10.4-11.1)	8.9 (8.7-9.2)	15.1 (14.7-15.4)	6.1 (5.9-6.2)	4.5 (4.2-4.6)
10 ♀	37.6 (35.5-39.2)	10.1 (9.9-10.5)	8.4 (8.0-8.7)	14.3 (13.8-14.7)	5.8 (5.4-6.2)	4.2 (4.0-4.4)
Margarita Island, Nueva Esparta, Venezuela						
1 ♂	—	10.0	8.6	14.6	5.9	4.1
1 ♀	38.6	—	8.6	14.9	5.9	4.0
San Antonio del Gulfo, Sucre, Venezuela						
1 ♂	36.9	11.0	9.1	15.5	6.0	4.4
1 ♀	35.2	—	8.8	14.3	5.7	4.2
Jusepin, Monagas, Venezuela						
5 ♂	38.9 (37.3-39.9)	10.4 (10.2-10.5)	8.5 (8.4-8.6)	15.1 (14.8-15.4)	6.1 (6.0-6.3)	4.4 (4.1-4.6)
5 ♀	38.4 (37.3-39.5)	10.1 (9.8-10.4)	8.4 (8.3-8.7)	14.5 (14.3-14.7)	5.9 (5.8-6.0)	4.2 (4.0-4.3)
Maripa, Bolívar, Venezuela						
5 ♀	33.8 (32.7-34.9)	10.0 ⁶ (9.8-10.1)	8.4 (8.2-8.6)	13.7 (13.5-13.9)	5.6 (5.4-5.7)	3.9 (3.8-4.0)

to comprise 50-60 species based upon field investigations by Smith and previous records; sixty species of bats were reported from Surinam by Husson (1962).

The only change in Koopman's (1958) rank order of islands based on the number of chiropteran species inhabiting them is Margarita, which is now known to have more species than Grenada. This could have been predicted by the fact that Margarita is a much larger and higher island as well as being a continental island rather than an oceanic island.

Among the 16 species which presently comprise the chiropteran fauna of Margarita Island there are two species of emballonurids, one noctilionid, two mormoopids, nine phyllostomatids, one vespertilionid, and one molossid. Within the family Phyllostomatidae, the subfamilies are represented as follows: Phyllostomatinae, 2; Glossophaginae, 2; Carollinae, 1; Stenoderminae, 2; Desmodontinae, 2. *Rhogeessa minutilla* Miller, 1897 and *Leptonycteris curasoae tarlosti* Pirlot, 1965 were described from Margarita Island; neither is currently regarded as unique to the

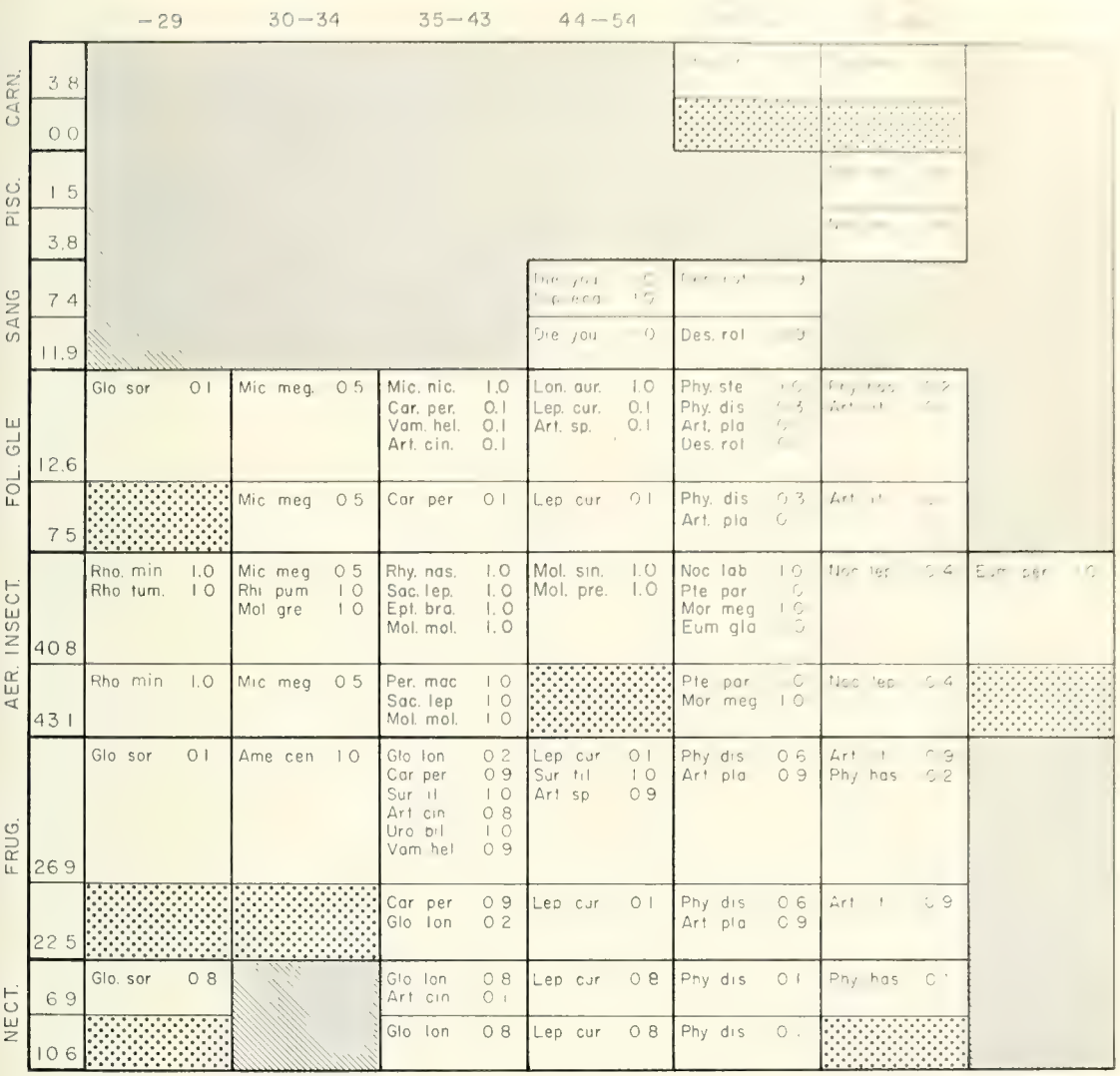


Figure 3. Composite, two-dimensional niche matrix for the 16 bat species from Margarita Island and the 39 species actually captured on the adjacent Venezuelan mainland. The trophic role values are those employed by Wilson (1973) or only slightly modified. The model values for forearm length are those used by Fleming *et al.*, (1972). Each of the 49 cells of the matrix is divided into two parts, the upper represents species (abbreviated scientific names) and trophic role values for the Venezuelan mainland and the lower represents those for Margarita Island. At the left-hand margin appear the importance values (IV) for each trophic role in each of the two regions. The importance values are derived by dividing the total trophic values by the number of bat species in each fauna and expressed as a percentage. Crosshatching represents "niches" that are apparently not occupied by the known chiropteran fauna of these regions. Dots represent "mainland niches" that are apparently unoccupied by the chiropteran fauna of Margarita Island. The dotted cells for aerial insectivores from Margarita may represent sampling biases.

island. All of these bats are Neotropical in their affinities and all are found on the adjacent Venezuelan mainland.

Notably absent from the chiropteran fauna of

Margarita Island are the three small, insectivorous families Natalidae, Thyropteridae, Furipteridae, and the frugivorous Sturnirinae (Phyllostomati-
dae), all of which occur in the chiropteran

fauna of the adjacent mainland. In addition it should be noted that no more than two species of each major taxonomic group are known from the island. The latter observation is particularly striking when considering the wide diversity of the Phyllostomatinæ and Stenoderminæ on the adjacent mainland (Fig. 3). Only in the case of *Artibeus planirostris* and *A. lituratus* is a genus represented by more than one species on Margarita Island. However, of the genera represented on the island, the following are represented on the mainland by two or more sympatric species: *Saccopteryx*, *Peropteryx*, *Noctilio*, *Pteronotus*, *Micronycteris*, *Phyllostomus*, *Glossophaga*, *Artibeus*, *Rhogeessa*, and *Molossus*. The apparent absence of some species of vespertilionids and molossids on Margarita may be an artifact due to the fact that these bats are not readily captured in mist-nets and extensive collecting in and around their potential roost-sites such as attics of buildings, rain spouts, and elsewhere, was not conducted. With the use of other collecting techniques we would anticipate the addition of other species of these two insectivorous families to the Margarita fauna.

As noted above, all of the species which inhabit Margarita Island also occur on the mainland of northeastern Venezuela. Only 13 of the taxa from Margarita have been recorded on Trinidad; the three exceptions are *Leptonycteris curasoae*, *Pteronotus parnellii fuscus*, and *Glossophaga longirostris longirostris*. The latter two species are represented on Trinidad by different geographic races; *P. p. rubiginosus* with its affinities apparently with the Amazon Basin fauna (Smith, 1972:76) and *G. l. major* apparently independently differentiated on Trinidad and Tobago. Compared with the chiropteran fauna of Surinam (Husson, 1962), only six taxa occurring on Margarita Island are presently known from that country also. Four, six, and four species found on Margarita also inhabit Aruba, Curacao, and Bonaire, respectively. Seven species are shared by Margarita and Grenada islands.

From the foregoing account, it should be apparent that the chiropteran fauna of Margarita Island represents an attenuation of a fauna characteristic of northeastern South America (including Trinidad).

The representation of most major taxonomic groups of bats on Margarita Island, but in markedly reduced numbers when compared to the adjacent Venezuelan fauna, may reflect (1)

the area of the island, (2) the proximity of the island to the source area, and (3) the ecological diversity of the island. These three factors have been discussed by Koopman (1958, 1968), MacArthur (1965), MacArthur and Wilson (1963, 1967), and others. More recently, McNab (1971), MacArthur, Diamond, and Karr (1972), and Fleming, Hooper, and Wilson (1972) have approached the problems of island faunas from the viewpoint of the ecological role of the individual species which comprise the fauna. Unfortunately, such studies are greatly limited by the paucity of available information on the ecological roles of many species; this is especially true of bats.

Inasmuch as the entire adaptive radiation of Neotropical bats seems to have revolved around diverse feeding habits, the availability of particular food sources and food items of particular sizes would appear to be primary parameters in the chiropteran niche. McNab (1971) also considered these two factors to be most important in the niche partitioning of tropical bat faunas.

A consistent classification of chiropteran food habits has not been readily available in the past and in fact, the food habits of many species simply are not known. Wilson (1973) made a noteworthy attempt at such a classification. In our analysis of the chiropteran fauna of Margarita Island and the adjacent mainland we have followed his method of categorizing the various species into trophic categories. These categories are (Fig. 3): carnivores (CARN.—feeding on tetrapods); piscivores (PISC.—feeding on fish); sanguinovores (SANG.—feeding on blood); foliage gleaners (FOL. GLE.—feeding on insects on foliage or on the ground); aerial insectivores (AER. INSECT.—feeding on flying insects); frugivores (FRUG.—feeding on fruit); and nectarivores (NECT.—feeding on flowers, nectar, and/or pollen).

For comparative purposes, we have categorized the trophic habits of the species comprising the fauna of Margarita and those of 39 species actually captured by Smith on the adjacent Venezuelan mainland. We have adopted Wilson's (1973) trophic values in most cases or only deviated slightly from his assessed value. In addition, our values are placed at the specific level rather than at the generic level.

A combined, two-dimensional niche matrix for the bat fauna of Margarita Island and the Venezuelan mainland is presented in figure 3. Several interesting points can be seen in this diagram.

TABLE 6. Importance values for the seven trophic roles of the chiropteran faunas of northern South America and the Antilles. The number in parentheses represents the number of species in each of the updated faunas; see text for citation.

	Carn.	Pisc.	Sang.	Fol. Gle.	Aer. Insect.	Fru.	
Aruba (4)	0.0	0.0	0.0	2.5	50.0	7.5	40.0
Curacao (8)	0.0	7.5	0.0	2.5	55.0	15.0	20.0
Bonaire (6)	0.0	0.0	0.0	1.6	50.0	21.7	26.7
Margarita (16)	0.0	3.8	11.9	7.5	43.1	22.5	10.6
Venezuela (39) ¹	3.8	1.5	7.4	12.6	40.8	26.9	6.9
Surinam (61)	3.7	1.0	3.2	10.8	48.0	23.8	9.5
Trinidad (63)	3.5	0.9	3.0	11.3	48.9	26.8	5.6
Tobago (17)	2.3	3.5	0.0	7.6	40.6	40.0	5.9
Grenada (12)	0.0	5.0	0.0	4.2	45.0	31.6	14.2
Dominica (12) ²	0.0	5.0	0.0	2.5	45.0	29.2	18.3

¹ Based on actual captures.

² Based on Jones and Phillips (1970).

The 39 mainland species occupy 29 of the 49 cells of the matrix and the 16 bats from Margarita occupy 20 of these cells. At this time it is difficult to comment on the "unoccupied" cells in both faunas. Future studies no doubt will reveal these to be either nonexistent or to be occupied by other terrestrial vertebrates. With respect to bat faunas in general, we doubt that the six cells in the upper left-hand corner (small-sized carnivores, piscivores, and sanguinivores) exist for bat species. This is based on problems of body size versus prey size and various physiological parameters. The unoccupied cells on the right-hand side of the matrix either reflect sampling biases or do not exist for bats in northeastern South America. With the exception of the sanguinivore cells, these unoccupied cells are indeed occupied by bats in other faunal regions.

McNab (1971:354) notes that carnivorous species of bats, other than fishing species, are generally absent from island faunas. He cites species of the genus *Phyllostomus* as the only carnivorous species on Margarita and Tobago. *Phyllostomus discolor* is the species occurring on Margarita, and to our knowledge is not a carnivorous species (Fleming *et al.*, 1972:559; Goodwin and Greenhall, 1961:238). Therefore, the carnivorous cells of Margarita Island at this time appear to be unoccupied by bats. The apparent absence of carnivorous bats on islands is further illustrated in table 6.

As can be seen in figure 3, the bulk of the bat faunas of Margarita and the adjacent mainland occupy the aerial insectivore-frugivore cells, 67.5 and 65.6 percent, respectively. In representative chiropteran faunas from northern South

America and the Antilles (Table 6) these trophic roles are also predominant with the aerial insectivore complement comprising the larger of the two.

Koopman (1958:434) points out that the ecological differences among the various islands off the northern coast of South America are rather extreme. Aruba, Curacao, and Bonaire, the most xeric of these islands, have a disproportionately large aerial insectivore and nectarivore fauna compared to that of Trinidad, Tobago, and Grenada, which are the most mesic of the islands. Margarita Island, which has both xeric and mesic conditions, is intermediate, at least with regards to the nectarivorous trophic role. The foliage gleaning trophic role appears to be reduced on all islands except Trinidad. There is a marked disharmony (MacArthur and Wilson, 1967:175-78) in the bat faunas of Aruba, Curacao, Bonaire, Grenada, and Dominica, as compared with the mainland fauna, as illustrated by the absence of carnivores and sanguinivores (Table 6). The Margarita fauna is disharmonic with the mainland in lacking carnivorous species as is Tobago in lacking sanguinivorous species. It should be pointed out that Trinidad essentially represents an extension of the mainland chiropteran fauna with all trophic roles being represented.

In conclusion, the bats of Margarita Island comprise a depauperate chiropteran fauna which is most closely allied to the adjacent Venezuelan bat fauna. Ecological diversity and the size of the island seem to be the most relevant factors influencing the composition of the Margarita fauna. The proximity to the source area, at least with regards to the islands off the north coast

of Venezuela, does not appear to be a major limiting factor for these respective faunas.

We believe that the reduced size of the Margarita bat fauna is a result of repartitioning or expansion of the mainland niches on the island. In examining increasing population density on species-poor islands MacArthur *et al.* (1972) note that species utilized more space (that is, wider range of altitude, or habitats, or vertical foraging strata, or any combination of these; wider range of foraging techniques; or broader utilization of food items). Although we do not have sufficient data relating to population densities of the chiropteran species from Margarita Island, we suspect that they also utilize wider niche space which might account for the reduced bat fauna of this island.

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MATERNITY HABITS OF *MYOTIS LEIBII* IN SOUTH DAKOTA

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ABSTRACT: Twelve active roosts containing 27 *Myotis leibii* were located in and near the Badlands National Monument, South Dakota. Active and inactive roosts were characterized as to temperature inside and outside of the roosts, position and size of opening, slope facing, internal dimensions, and soil type. Two roosts each contained more than two individuals; all others held single individuals or a single female and her young. A possible instance of twinning was observed. Young bats were characterized as to weight, length of forearm, amount of pelage, and flying ability.

Although *Myotis leibii* was first recognized more than 100 years ago, little is known concerning its summer roosting habits. Only one maternity colony has been reported and other observations of summer roosting have been limited. Koford and Koford (1948) reported a colony of at least 35 individuals, including juveniles, roosting under wallpaper in an abandoned wooden house in California. The only other summer colony recorded was an estimated 12 individuals roosting behind a sliding shed door in Ontario (Hitchcock, 1955). Other bats of this species have been found roosting alone or in pairs under the following circumstances: between boards leaning against the wall of a cottage (Stephens, 1945); in barns (Jones, 1964:84); under a loose strip of pine bark (Swenk, 1908:137; Jones, 1964:84); under a large flat rock at the edge of a quarry (Tuttle, 1964); under a stone on a hillside; in erosion crevices in the Badlands of South Dakota (Barbour and Davis, 1969:103); and in small pockets of eroded sandstone in the Badlands of Nebraska (Quay, 1948).

Between 21 and 29 July 1972, we spent 30 man-hours searching for roosts of *M. leibii* in and near the Badlands of South Dakota. Twelve of the more than 35 roosts (places containing guano) discovered were occupied by a total of 27 bats including seven lactating females, two postlactating females, one nonreproductive female, one adult male, four juvenile females, and seven juvenile males (Table 1). Five individuals escaped before sex or age could be determined. There was no evidence that the bats had altered the naturally formed roosts they occupied.

Age of juveniles varied appreciably. The smallest weighed 1.6 gm and had a forearm length of 14.5 mm; the heaviest weighed 3.9 gm and had a forearm length of 31.0 mm. Only the largest

juvenile was volant and it could not maintain flight for more than 100 m. Six juveniles were nonvolant (forearms 14.5–24.5), and four were capable of slight forward progression (forearms 27.0–30.0) when released a few feet above ground level. Extremes for forearm lengths and weights for juveniles follow: females, 14.5 mm–31.0 mm and 1.6 gm–3.9 gm; males, 17.5 mm–29.0 mm and 1.9 gm–3.8 gm. The smallest female had no body fur, and one male was only slightly furred; all others were moderately to completely furred.

Only two roosts contained more than a single adult or an adult and its offspring. Roost number 3 held four lactating females nursing five nonvolant juveniles; one female apparently was nursing two juvenile males having the same weight and forearm length. *Myotis austroriparius* is the only member of this genus in the United States so far reported to produce twins (Barbour and Davis, 1969:61), but we interpret our findings as an indication of twinning in *M. leibii*. Roost 11 contained a postlactating female in addition to a lactating female and her single offspring. Adult males were absent from areas where females and their juvenile offspring were found; the single adult male, taken in roost number 1, was roughly $\frac{1}{4}$ mi from the nearest other roost that was located.

Roosts 1 and 2, at ca. 4 mi E Cottonwood, Jackson County, were in horizontal fractures in large, flat, siltstone boulders that measured 0.3 m $\times$ 1 m and 0.75 m $\times$ 2 m, respectively (Fig. 1). A farm pond approximately $\frac{1}{4}$ mi N was the nearest source of water. Roost number 10, near

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Figure 1. Roost number 1 was located in large rock in center right of photograph.

TABLE 1. Characteristics of roosts occupied by *Myotis leibii*.

Roost Number	Date	Time	Temperature (°C)		Entrance Location	Entrance Size	Maximum Inside Dimensions
			in Roost	Outside			
1	21/7/72	1800	29	30	Horizontal crack in rock on hillside	1.5 × 9.0 cm	1.5 × 9.0 × 14.0 cm
2	25/7/72	1505	26	32	Horizontal crack in rock on hillside	1.5 × 2.5 cm	1.5 × 25.0 × 15.0 cm
3	24/7/72	1230			Hole on 15° angle near hilltop	2.5 × 3.5 cm	2.0–3.5 × 15.0 × 31.0 cm
4	26/7/72	1220	26	29	Face of vertical bank	2.5 × 3.5 cm	2.5 × 2.5 × 5.0 cm
5	26/7/72	1300	28	31	Face of vertical bank	1.5 × 2.5 cm	1.5 × 20.0 × 20.5 cm
6	26/7/72	1400	26	33	Face of vertical bank	3.5 × 3.5 cm	1.5–3.5 × 28.0 × 28.0 cm
7	28/7/72	1350	28	29	Hole 5 m up hillside on 80° slope	2.0 × 2.5 cm	2.0 × 2.5 × 6.0 cm
8	28/7/72	1410	27	29	Face of vertical bank	4.5 × 6.5 cm	2.5 × 3.0 × 20.5 cm
9	28/7/72	1530	33	29	Face of vertical bank	1.5 × 2.5 cm	2.0–2.5 × 5.0 × 6.0 cm
10	28/7/72	1730	27	28	Hole 1.5 m up hillside on 80° slope	2.5 × 2.5 cm	2.5 × 6.0 × 2.5 cm
11	29/7/72	1735	29	35	Face of vertical bank	2.0 × 3.5 cm	3.0 × 8.0 × 48.0 cm
12	29/7/72	1830	28	34	Hole in top of vertical shelf 10 m up 50° hillside	2.0 × 2.5 cm	2.5 × 4.0 × 4.0 cm
Means			28	31		2.3 × 3.7 cm	2.3 × 10.7 × 16.7 cm

* Mean volume of roosts was 411 cc.



Figure 2. Badlands habitat where *Myotis leibii* roosted.

Norbeck Pass in the Badlands National Monument, Pennington County, was located in a small crevice in a very hard, whitish-gray Oligocene sediment. Other roosts were found at a place $8\frac{1}{4}$ mi S, $4\frac{1}{4}$ mi E Wall, Pennington County, where a mixture of clay and volcanic ash of early Miocene age had been eroded to form small crevices and cavities in the nearly bare hillsides (Fig. 2). The ground surface was porous and contained abundant cavities of the kind used by *M. leibii* for roosting. Roosts were found exclusively in the Miocene sediments and none was encountered in the softer, less durable layers of reddish Oligocene sediments. These formations are located in open grassland; ponds covering areas of roughly 1, 4, and 6 acres are 0.3, 1, and 2 mi distant, respectively.

Six of the twelve occupied roosts were located in crevices in the walls of vertical banks an average of 170 cm (range 51–340) above dry streambeds but others were less uniformly situated (Table 1). Directional data were recorded for nine of the twelve occupied roosts. Six were located on west facing slopes, two faced southwest, and one faced south. Depth below ground surface varied from

2.5 to 20.5 cm with an average depth of 6.5 cm (Table 1). Roost number 3, near the top of a 75° hillside, was 20.5 cm below ground surface, and differed from most other roosts in that the surface received direct sunlight from midmorning until late evening. The shallowest roosts were in positions that received only a few hours of direct sunlight daily.

Myotis leibii apparently exercises considerable selectivity in choice of roost sites. In addition to being characteristically small, dry, and shallow, occupied roosts seemed to be of fairly uniform high temperature. Temperature was measured from a point near the center of the inner wall of the roosts between 1215 and 1830 (Table 1). Afternoon temperatures probably are near the upper extreme, but unfortunately do not reflect range in temperatures tolerable to a maternity colony of this species.

Average wall temperature in seven maternity roosts was 27°C (range 26–29), whereas, that in four nonmaternity roosts was 29°C (range 27–33). Temperatures in maternity roosts (2–6, 8, and 11–12) averaged 5°C lower than outside air temperatures taken 1 m distant in the shade,

but in each of three nonmaternity roosts (1, 7, and 10) it was only 1° below outside ambient temperatures. Temperature in the fourth nonmaternity roost, number 9, was 4° C above ambient (Table 1). The average temperature in five unoccupied roosts (guano present) was 30° C (range 29–31), but that in a sixth was only 23° C. Crevices of various size with temperatures as low as 20° C were abundant in the Badlands area, but none of these cooler chambers evinced occupation by *M. leibii*.

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INFLUENCE OF HABITAT STRUCTURE ON A POPULATION OF VOLES

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ABSTRACT: Analysis of dispersion patterns for a population of the California vole (*Microtus californicus*) within its preferred habitat indicated higher densities associated with patches of a perennial grass (*Elymus cinereus*) than with the dominant annual (*Bromus rigidus*). Although this pattern occurred throughout the year, the only demographic differences between subpopulations occurred during the warm, dry summer. More adult (heavier) voles were found in *Elymus* during August, a result of improved survival and growth. The greater availability of preferred food (green forage) in *Elymus* patches suggested that the demographic improvement resulted from better nutrition. Such patches serve as refugia for voles when populations are low, thus assuming increased significance.

The preference of voles for grassland and meadow habitats is well known, and vegetational characteristics seem to influence the dispersion and density of voles within their preferred habitats (Batzli, J. Mamm., 49:239–250, 1968; Getz, Univ. Connecticut Occas. Pap., Biol. Sci. Ser., 1:

213–241, 1970). In addition, dispersal out of more favorable habitats may be an important

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TABLE 1. Dispersion of *Microtus* in relation to *Elymus*.

Trapping period	Number of individuals captured	Expected in <i>Elymus</i> number (percent)	Observed in <i>Elymus</i> number (percent)	Chi-square 1 d.f.	P
Jan.	110	18.6(16.9)	34(30.9)	15.3	<0.01
Mar.	79	13.3(16.9)	23(29.1)	8.5	<0.01
May	117	19.8(16.9)	35(29.9)	14.0	<0.01
Aug.	56	9.5(16.9)	24(42.9)	26.6	<0.01
Nov.	61	10.3(16.9)	20(32.4)	11.0	<0.01
Jan.-Nov.	302	51.0(16.9)	86(28.4)	32.1	<0.01

factor limiting the population growth of voles (Krebs *et al.*, Sci., 179:35-41, 1973). In spite of these conclusions, there are few cases that show differences in the demography of voles which are clearly associated with characteristics of the natural vegetation within preferred habitats. This report presents such a case for the California vole (*Microtus californicus*).

METHODS

The study site was located at the Russell Property of the University of California ten miles east of Berkeley. A 0.4-hectare grid was staked at 7.5-m intervals in a peninsula of annual grassland which was bordered by oak woodland (*Quercus agrifolia*) and chaparral (*Adenostoma fasciculatum*). Most of the grid was dominated by ripgut brome (*Bromus rigidus*), but patches of wildrye (*Elymus cinereus*) covered about 10 percent of the grid. A photograph and a quantitative description of the vegetational composition of the site may be found in Batzli and Pitelka (Ecol., 51:1027-1039, 1970).

Demographic data were gathered by means of live trapping. Longworth traps were set at each station in the grid; two per station. Voles were ear tagged, weighed, examined for reproductive condition and released at the point of capture. Five trapping periods of 3-4 days each were completed in 1968. Details of the trapping methods can be found in Batzli and Pitelka (J. Mamm., 52:141-163, 1971).

Thirteen of the 77 trapping stations (16.9 percent) were located in or next to sizable patches of *Elymus*. The vole population was divided into two subpopulations depending on the location of captures. One subpopulation is considered to be associated with *Elymus* because half or more of their captures were at stations in *Elymus*, and the remaining subpopulation consists of associates of *Bromus*.

RESULTS AND DISCUSSION

Both the densities and structure of the subpopulations were examined. First, I tested the hypothesis that the densities of voles were evenly distributed between *Bromus* and *Elymus*. If this were true, 16.9 percent of the voles should be associated with *Elymus*. Table 1 shows the results of chi-square tests for each trapping period and for the year as a whole. In all cases more voles were associated with *Elymus* than expected. Another mouse present on the grid, the harvest mouse, *Reithrodontomys megalotis*, did not have higher capture rates in *Elymus*.

Second, I tested the hypothesis that the proportion of females and the proportion of adults in the subpopulations were the same. Adults were defined as female voles weighing 35 g or more and male voles of 40 g or more. Table 2 shows the result of chi-square tests of homogeneity. In all cases but one the hypotheses were accepted. In August, the warmest and driest month, a significantly larger proportion of adults was present in the subpopulation in *Elymus*.

Analysis of movements indicated no net movement into the *Elymus*, so the explanation for the higher density in *Elymus* was sought by examining reproductive and survival patterns. Seasonal trends in the reproductive activity of females were evident in both subpopulations, varying from 17 percent with enlarged teats in August to 100 percent with enlarged teats in March. How-

TABLE 2. Structure of population in *Elymus* and in *Bromus*. Values for *Bromus* are in parentheses.

Sample period	Number of voles	Percent females	Percent adults
Jan.	34(76)	56.6(59.2)	41.2(38.2)
Mar.	23(56)	60.9(55.4)	78.2(75.0)
May	35(82)	77.1(58.5)	40.0(34.1)
Aug.	24(32)	62.5(56.2)	70.8(21.7)*
Nov.	20(41)	55.0(63.4)	95.0(82.9)

* P < .05, chi-square test of homogeneity.

TABLE 3. Survival rates of *Microtus* in *Elymus* and in *Bromus*. Values for *Bromus* are in parentheses.

Dates	Number in cohort	Proportion survived between dates	P
Jan. 21/Mar. 11	28(69)	.429(.405)	.616(.59)
Mar. 11/May 15	19(53)	.421(.302)	.688(.59)
May 15/Aug. 19	30(70)	.534(.272)*	.833(.683)
Aug. 19/Nov. 13	18(32)	.722(.562)	.899(.827)

* $P < .025$, chi-square test of homogeneity.

ever, no significant differences were found between subpopulations. Indeed, the percent of females with enlarged teats for all five samples was nearly the same, 80.0 percent for voles in *Elymus* and 83.5 percent for voles in *Bromus*. Analysis of minimal survival rates showed that survival was significantly better in *Elymus* than in *Bromus* during the early summer (Table 3). Changes in minimal survival probably reflect changes in mortality rates rather than dispersal because the study site was surrounded by unfavorable habitat on three sides. This improved survival can account for both the increased proportion of adults in the August sample and for the higher densities in *Elymus*.

Several plausible explanations for the increased survival in *Elymus* can be suggested. *Elymus* is a robust perennial grass which remains green during the early summer after the annual grasses have dried. Voles normally eat green grass when available. Vegetation was point-sampled at 15 randomly selected stations during the year (Batzli and Pitelka, 1970). In August one station was in *Elymus*, and it showed that *Elymus* was taller and provided more cover during the summer than *Bromus*, as was clear from visual inspection. Average height of the vegetation for the grid as a whole was 11.8 cm while for *Elymus* it was 29.8 cm. Percentage cover for the grid as a whole was 41.3 percent while for *Elymus* it was 52.5 percent. Thus the *Elymus* might aid survival by improving nutrition, by protection from predation and by providing a more favorable microclimate.

Unfortunately, because the results were unexpected, no measurements of predation or microclimate were made, but some evidence can be related to the nutritional explanation. Analyses of stomach contents showed that with the drying of annual grasses, *Microtus* switched their diet from green grasses to grass seed, and breeding declined. Occasional meals of green herbs, including *Elymus*, were still taken (Batzli and Pitelka, J. Mamm., 52:141-163, 1971).

Common responses to improved nutrition are improved survival, improved reproduction and improved growth, and experiments in the laboratory showed that voles on natural seed diets had poorer survival, reproduction and growth of young than voles on natural grasses (Batzli, in prep.). Since few green materials were present in the portion of the grid with *Bromus*, the portion with *Elymus* seemed to provide higher quality food.

As indicated earlier the adult females in the *Elymus* did not show better reproduction, but because of the larger number of adults, the mean weight of voles in *Elymus* was higher than in *Bromus*, 38.8 ± 1.2 g ($n = 21$) vs. 33.9 ± 1.2 g ($n = 23$; $p < 0.01$, t -test). Larger size seemed to be related to improved growth of young during early summer as well as improved survival. Mean weight increase of young between May and August was 10.8 ± 2.5 g ($n = 9$) in *Elymus* and 7.3 ± 2.0 g ($n = 10$) in *Bromus* ($0.15 < p < 0.10$, t -test). Thus there is some evidence that demographic improvements were related to better nutrition.

Such subtle influences of vegetational structure may have great importance for population processes in voles. It is just such patches of more favorable habitat which serve as refugia during population lows of the California vole (F. A. Pitelka and O. P. Pearson, pers. comm.). Elucidation of the exact role of favorable patches of vegetation in the population dynamics of voles should be determined by manipulation of the quality, size, and dispersion patterns of refugia.

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AN UNUSUAL BREEDING AGGREGATION OF FROGS, WITH
NOTES ON THE ECOLOGY OF *AGALYCHNIS SPURRELLI*
(ANURA: HYLIDAE)

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ABSTRACT: In August 1970, a breeding aggregation comprising an estimated 13,000 *Agalychnis spurrelli* was observed at a man-made pond on the Osa Peninsula, Puntarenas Province, Costa Rica. Apparently this extraordinarily dense breeding population was the result of ideal conditions offered by the artificial breeding site: the lack of the more effective predators (fish) in a large permanent body of water surrounded by numerous suitable oviposition sites and continuous forest which is immediately accessible for post-metamorphic dispersal. A high degree of larval success followed by normal post-metamorphic mortality, unaffected by density dependent factors, could lead to the high breeding population observed. Some males at the site were seen to scrape previously laid eggs off leaves. Additional observations and experiments demonstrated a definite parachuting ability of *A. spurrelli*, a behavioral and morphologic adaptation shared to a greater or lesser degree with other highly arboreal tree frogs.

Breeding choruses of phyllomedusine hylid frogs are generally small and consist of a few males widely separated and apparently not interacting. In fact, Pyburn (1970) stated that for *Agalychnis callidryas*, even at the breeding peak, a distance of at least 50 cm is maintained between calling males, with no two ever calling from the same perch; and Breder (1946) never heard more than five males of this species calling in any one chorus. Our experience with *Agalychnis dactylos*, *A. callidryas*, *A. moreletii*, *A. spurrelli*, *A. saltator*, *A. annae*, and *Phyllomedusa lemur* confirms these observations. *Agalychnis spurrelli* was considered to be a rare frog in Colombia by Cochran and Goin (1970) and Duellman's (1970) comprehensive review listed only 47 specimens from Middle America with a maximum of 12 (taken at different times) from any one locality. Boulenger (1913) first described the egg-laying of *A. spurrelli* (from Spurrell's notes), which follows a basic phyllomedusine pattern of placing the eggs on the leaves of trees overhanging ponds and pools.

Thus we were startled when, in full daylight, we encountered an enormous breeding aggregation of thousands of individuals of *A. spurrelli* around a small artificial pond on the Osa Peninsula, Puntarenas Province, Costa Rica. The population was so dense that frogs were crawling over and knocking each other out of the breeding trees and males were scraping eggs from leaf surfaces. The magnitude of the breeding aggregation gave

us opportunity for insight into the little known biology of this species and for speculation regarding the causes of what we suggest is an abnormal population phenomenon. Thirty-three frogs were collected from the aggregation and are now deposited in the Natural History Museum of Los Angeles County, the Museo de Zoología, Universidad de Costa Rica, and The University of Connecticut Museum of Zoology.

Description of the frog: *Agalychnis spurrelli* is a member of what is considered to be one of the most arboreal of the tree frog genera (Duellman, 1968). This species has a white-spotted yellow-green dorsum, bright orange flanks, feet and venter, burgundy-red eyes and a thin body with long spindly legs (Duellman, 1970, pl. 43), although eleven of 22 animals of both sexes in our series lacked the dorsal white spots used as a key character by Duellman (1970). In addition, *A. spurrelli* is distinguished by having exceptionally well-developed webs between the toes, especially on the front feet (Savage and Heyer, 1969). It is a large tree frog; the mean length of 23 males in our series was 49.7 mm (range, 46–53), and the 10 females 62.4 mm (57–67). Adult frogs of this species from the

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Osa locality are smaller than specimens from the other known locality for *A. spurrelli* in Costa Rica and from Panama (Duellman, 1970). By our measurements, twenty-five Osa males are significantly ($p < 0.01$, Median test) smaller than nine males from the Dominical Road (16 km SW San Isidro de El General, Puntarenas Province, Costa Rica in the collection of the University of Southern California); two females taken at the latter locality are at least 2 mm larger than our largest female.

Description of the study area: The pond around which the frogs were observed is located at an elevation of less than 50 m, near the Mile 4 marker on the Lowland Road to the Pacific, not far from the Rincón de Osa airstrip, on the Osa Peninsula, Puntarenas Province, Costa Rica. This is in an area of high rainfall (approx. 3500 mm/yr) with a short definite dry season, and warm temperatures (usually above 19°C). Evergreen species predominate in the surrounding forest; most trees hold a good crown of leaves during the entire year.

The pond was formed by roadbuilding activities of the local lumber company, Osa Productos Forestales, probably in the late 1950's or early 1960's. In August, 1962, entomological and herpetological collections were made in and around the pond by members of University of Southern California and Los Angeles County Museum-USACR field parties (Starrett and Casebeer, 1968) and since then biologists from various institutions, including the Organization for Tropical Studies, have visited the site for one purpose or another. Beginning in 1968, the senior author has done limited collecting and made observations at the pond semi-annually, during the dry and wet seasons. The pond, which lies about 100 m from the road, is roughly oval in outline, 70m x 50 m, and it has an area of open water in the center which is surrounded by flooded grass or primary forest (Fig. 1). The greatest depth of the pond seasonally fluctuates between about 1.0 and 2.8 m. The dry season ordinarily includes part of January, February, and March, but in 1970, the dry season was cut short by an exceptionally early and wet rainy season and we found the pond to be at the highest level that we had ever seen it (2.8 m in the deepest part).

Potential egg and tadpole predators, except fish, are common. The water is clear and extensive seinings and day and night observations during high and low water periods have failed to reveal any fish, but dragonfly nymphs, dytiscid

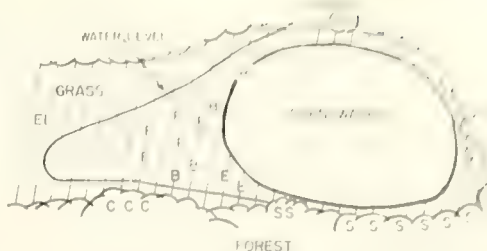


Figure 1. Diagram of breeding site ("Caiman Pond") on Osa Peninsula, Costa Rica. Letters represent areas in which calling or amplexing frogs were observed or heard. August 10-12, 1970. B, *Hyla Boulengeri*; C, *Agalychnis callidryas*; E, *H. ebraccata*; El, *H. elaeochroa*; P, *Leptodactylus pentadactylus*; R, *H. rosenbergi*; S, *A. spurrelli*.

beetles and aquatic hemipterans are abundant. Least Grebes (*Podiceps dominicus*) have been on the pond at each semi-annual observation since 1968. In July 1969 there were flightless young present and in August 1970 there were two pairs of grebes with young. A pair of Purple Gallinules (*Porphyryla martinica*) also had young and a Green Heron (*Butorides virescens*) was building a nest at the pond margin. On August 10, we watched the adult gallinules eating the eggs of *A. spurrelli* up in the vegetation and a single Green Kingfisher (*Chloroceryle americana*) was observed to catch and eat many *A. spurrelli* tadpoles while we were working at the pond on August 10-12. A large female caiman (*Caiman crocodilus*) hatched young at the pond margin in August 1968 and 1969, but there was no evidence of a nest in 1970. However, on August 10, 1970 a large caiman was present and a single hatchling was captured at night while apparently stalking a calling *Hyla Boulengeri*. The rather regular occurrence of caimans at this locality since 1962 gave rise to the name "Caiman Pond" which is used by many biologists familiar with the area.

Amboreal snakes, *Imantodes* spp. and *Leptodeira septentrionalis* are known egg predators. The latter has been recorded preying on eggs of *A. moreletti* (Smith, 1943) and *A. callidryas* (Duellman, 1958; Pyburn, 1963) and we have seen this species three times in breeding choruses of *A. callidryas* on the Osa Peninsula. Students in other years have observed *Imantodes* preying on *A. callidryas* eggs at other breeding sites not far from the pond. Fly maggots were present



Figure 2. Photograph of vegetation at breeding pond, with *Agalychnis spurrelli* and egg masses, Osa Peninsula, Costa Rica, taken on the morning 10 August, 1970. At least 20 *A. spurrelli* may be found in this picture.

in a few old egg masses containing dead eggs, on August 10, 1970.

Several frog species in addition to *A. spurrelli* were calling in or around the pond during some of the August 1970 observation periods (*Hyla ebraccata*, *H. rosenbergi*, *H. elaeochroa*, *H. Boulengeri*, *Agalychnis callidryas*, and *Leptodactylus pentadactylus*) and the tadpoles of *H. ebraccata*, *H. Boulengeri*, *A. spurrelli*, and *Leptodactylus poecilochilus* were seined from the pond. Large tadpoles of either (or both) *A. callidryas* or *A. spurrelli* were in the pond in March 1970 and Lynch (Duellman, 1970, p. 127) took tadpoles of *A. spurrelli* there in early August 1967.

Observations of frog activity: On August 9, hard afternoon thundershowers broke a short dry spell of several days and frogs were exceptionally active during the night following the rains. At 0600 on August 10 a low, seemingly distant frog chorus, emanating from the direction of the pond, could be heard from the road. When we reached the pond, the chorus still seemed to be distant but, now, nondirectional. After a moment constant motion drew our attention to the trees

overhead. They were literally seething with adult *A. spurrelli* (Fig. 2). Most of the frogs were moving back into the trees from branches over the pond, but there were many frogs moving opposite to the general trend. Males formed a majority of the frogs, but many females, both free and in amplexus, were present. Occasionally a frog would fall from the trees into the pond.

The frogs were concentrated in three areas composing 10 m, 50 m, and 4 m of the pond margin (Fig. 1). Frogs covered the vegetation from the water level to 10 m high, but they were most densely packed on the lowest branches over the pond (1.5–3.0 m above the water). We estimated conservatively that there were 200 frogs per meter of occupied shoreline, with about 13,000 frogs in the total concentration. At the time that they were discovered at 0600, the frogs were gradually abandoning the breeding foliage by climbing, walking and jumping up and back along the tree branches. By 0910 sunlight had begun to strike the area and all frogs were gone from foliage over the pond. The tremendous frog concentration was dissipating into the surrounding forest.

Frogs leaving the area of egg deposition tended to go up for several meters before moving laterally into the forest and away from the pond. Continuous processions of frogs were seen on several occasions climbing straight up along lianas for 5–10 m. Unfortunately we were unable to follow any of the horizontal movement in the canopy far enough to determine how far they moved from the edge of the pond.

The distribution of calling males of other frog species in the pond is presented graphically in figure 1. It is significant that the males of *A. callidryas*, which has a breeding biology similar to *A. spurrelli*, were in trees overhanging a shallow, grassy portion of the pond, completely separated from the open water breeding localities of *A. spurrelli*.

Observations were continued until 1100 on the morning of 10 August, from 1800–1930 during a light rain on the evening of 10 August, from 0600 to 0700 on 11 August, and from 0700 to 0800 on 12 August. Eggs were collected for observation during the first and last periods. A few tadpoles were netted on the morning of 10 August and an intensive tadpole survey was made by seining on the morning of 15 August.

Male frogs were observed carrying out four distinct activities: calling, amplexus, moving in or out of the egg deposition area and leaf scraping.

Calling males usually were perched on a small branch in the egg deposition area. The call was a very weak, somewhat erratic *wuk! wuk! wuk!* given continuously. Two counts gave a note frequency of 150/min. This call is very different from the single, low-pitched groan which is the reported mating call of *A. spurrelli* (Duellman, 1970), and it may have been the "chuckle" call that Pyburn (1965, 1970) interpreted as a bluff attempt of a male *A. callidryas* in the presence of another male. The chorus was audible as a low murmur at least 100 m away because of the large number of calling frogs. Nothing resembling the usual *A. spurrelli* mating call was heard in the aggregation, although several phyllomedusine "chuck" calls heard near the pond were traced to *A. callidryas* males.

Almost all of the female frogs present were in amplexus. There did not appear to be any competition for the females, such as that noted by Pyburn (1965) in other species, but at the time of the observations most of the frogs were moving away from the breeding areas. Females seemed to constitute less than 10 percent of the aggregation. No egg laying activity was observed. There was no tendency to form a folded-leaf nest as suggested by Boulenger (1913).

Leaf scraping was observed on three different occasions with different males. A single male would back down, position himself in the center of a leaf covered with eggs, then proceed to remove the eggs with alternating sets of rotary scraping motions of the hind feet.

On the morning of 11 August, there were only about half as many frogs in the trees as the previous morning. By 0600 the breeding trees were almost deserted. On the morning of 12 August there were no frogs visible in the trees at 0700.

Egg masses: Egg masses literally dripped from the foliage. The densest egg mass concentrations were 1.5–3.0 m above the water, but clusters could be seen as high as 8 m. Some low bushes were extensively covered (Fig. 3). When first observed on 10 August, the masses appeared to consist of eggs of two ages, probably those laid the previous night (Aug. 9–10) and those laid the night of August 8–9. In addition, there were remnants of old, hatched egg masses. Those taken to the lab started hatching the night of 14 August, 6 days after the probable date of oviposition.

Most egg masses were on the upper surfaces of leaves. Attempts were made to count the number of eggs in individual "clutches" in the



Figure 3. Photograph showing egg masses of *A. spurrelli* at an area of near-maximum density. Time and location as in figure 2. At least 8 frogs, including one pair in amplexus are visible.

sense of Pyburn (1970) and Duellman (1963a). Counts of 14 clutches varied between 14 and 67 eggs (median 41), implying multiple clutches by individual females as Pyburn (1970) found for *A. callidryas* and *A. dacnicolor*. One leaf 30 x 11 cm taken from near the center of egg mass concentration had 533 eggs on the upper surface and 83 on the lower surface—a total of 616 eggs on one leaf. Thus, the total number of eggs in the breeding area is impressively large.

On the morning of August 11, many of the egg masses that had been present the day before had been scraped off of the leaves and in some cases new egg masses had been put in their place. The ground and water under the trees were strewn with fragments of egg masses with unhatched eggs. Eggs submerged in water invariably fail to hatch (Pyburn, 1970). There were almost surely fewer total eggs in the trees on August 11 than there were on August 10. We believe that most of the egg loss was from *A. spurrelli* males scraping them off of the leaves rather than loss to predators. Although there were no frogs in the trees the morning of August 12, there were a number of fresh egg masses from the night before.

Tadpoles: Dipnets and a seine were used to sample the tadpole population of the pond. On August 10, *A. spurrelli* tadpoles were found in several areas of the pond. Most of the tadpoles were fairly large (45 mm), but under the nesting trees a small, newly-hatched age class was netted (18 mm). Assuming that their development is similar to that of *A. annae* (Duellman, 1963b), these were about 72 days (stage 36) and 10 days (stage 25) old respectively. The tadpoles showed the typical phyllomedusine behavior of "hanging" head up in the open midwater, and they tended to aggregate in patches of open water in the grassy pond margin. Seining in very grassy portions of the pond yielded few *A. spurrelli* tadpoles.

Populational considerations: Occasional high densities of frogs have been noted since Biblical times (Turner, 1962). The members of these populations almost always have been recently-metamorphosed animals, usually near the rearing ponds, e.g. Gadow (1901) *Bufo bufo* and *Hyla arborea*; Dickerson (1907) *Bufo americanus*; deWitte (1948) *B. bufo*, *H. arborea*, *Rana temporaria*; Martof (1956) *Rana clamitans*; Waldron (1953) *Rana pipiens*; Scott (personal observations) *Bufo boreas*, *Bufo marinus*, *Bufo melanochloris*. Turner (1962) stressed the abnormality of these very dense concentrations, and Savage (1962, p. 67) suggests that the occasional reports of thousands of young frogs leaving the ponds at metamorphosis represent cases of unusually high tadpole survival. Evidently, there is a wide variation in ecological factors from pond to pond, species to species, and year to year (Turner, 1962; Savage, 1962).

The lack of conspicuous swarms of metamorphosing frogs in a pond that has received a large amount of spawn indicates a high tadpole mortality. The regular presence of normal breeding choruses coupled with swarms of juveniles means that there is a high juvenile post-metamorphic loss. These appear to be the most commonly encountered situations.

A third possibility, an abnormally dense breeding aggregation such as is reported here, is rarely observed. A breeding congregation of more than 45,000 *Hyla* (= *Smilisca*) *baudini* reported by Gadow (1908, p. 75) in Veracruz, Mexico, is one of the few detailed accounts of this phenomenon. Recent reports of "frog wars" in Malaysia are probably similar events (Smithsonian Institution, 1970). These dense, adult populations are a result of unusually low tadpole or juvenile mortality or both. In the present case,

increased egg loss is the only obvious high mortality factor positively correlated with density. As noted above, *Agalychnis* breeding choruses usually are composed of a few individuals. What then are the factors contributing to an apparently unique situation in this population of *A. spurrelli*?

In our experience, *Agalychnis* breed in temporary ponds containing few or no fish and the tadpoles are only subject to predation by birds and aquatic insects, and to the risk of desiccation in the event of an unseasonable dry spell. Scott (unpubl.) has data to indicate that *Agalychnis callidryas* tadpoles are extremely vulnerable to fish predation, presumably because of their mid-water habitat, and Wassersug (1971) has indirect evidence for a lack of effective poison glands in the larvae of *A. spurrelli*. Thus, larval mortality in permanent bodies of water usually would be high. The *A. spurrelli* discussed here are breeding in a recently manmade permanent pond that lacks fish. It is unusual for a natural, permanent, low-land tropical pond to lack fish for any great length of time and we have in the present case, a large-scale experiment showing the effects of providing optimal tadpole habitat without the uncertainty imposed by irregular droughts.

With a great production of juvenile frogs, unusually high mortality levels in the prebreeding stage would be required to prevent giant breeding aggregations. The forest surrounding the pond has not been greatly disturbed and chances for the survival of widely dispersed young frogs appear to be normal.

Bradford *et al.* (1950) found that some penned *Rana temporaria* and *Bufo bufo*, at densities as great as 50–100 per square meter, maintained themselves without appreciable loss of condition on foods that naturally came into the pens. Savage (1952) concluded from this that the non-breeding range of these two species could support many more animals than it does. Probably this also is true for *A. spurrelli*, since we rarely find non-breeding adult hylid frogs in the forest at night.

Most changes in animal populations are buffered by mortality factors that are positively correlated with population density. These density dependent factors are largely avoided by adult *A. spurrelli*. To be density modulated, a population requires input of information concerning the size of the population, but, since *A. spurrelli* adults spend most of their time in the forest, presumably isolated, this information can only be transmitted during the egg and tadpole stages and during

breeding aggregations. The egg stage was observed to suffer loss from both predators and leaf-scraping frogs. Leaf-scraping, at least, is density dependent. A similar type of egg loss has been documented in *Iguana iguana*, where large numbers of these big lizards nest on a tiny island, and nesting females often destroy previous nests (Rand, 1968). Tadpoles also were attracting some predators, but their impact on the total population is probably small. No predators were observed feeding on the adult breeding frogs. Thus the pond is probably producing juvenile frogs at a rate close to its carrying capacity and the young frogs disperse widely into the surrounding forest to grow into adulthood undecimated by density dependent mortality.

Thus, *A. spurrelli* appears to have built up a giant breeding aggregation by, 1) avoiding fish predation in the tadpole stage, 2) avoiding tadpole desiccation associated with temporary ponds, and 3) avoiding density dependent adult mortality by rapid and wide dispersal.

The first two conditions are a result of breeding in a man-made permanent pond, the third is a characteristic of the species. In addition, the breeding aggregation is concentrated by the relative scarcity of foliage overhanging the pond. Most pond-breeding frogs are able to use large areas of the pond (or at least the entire perimeter) for egg deposition, but *Agalychnis spurrelli* is limited to breeding in the trees and shrubs that extend over open water portions of the pond.

Parachuting: Frogs falling from the breeding trees were observed to alter their point of landing by parachuting. When falling into the pond, the animals assumed a rigid position with legs and digits spread. At about 2 m elevation the spread frog would execute a definite turn from the original direction of the jump, and glide back towards the pond margin. When the frog landed in the water, it would swim vigorously to the edge and climb up on the vegetation.

In order to examine this behavior more closely, we tested 31 adult *A. spurrelli* by forcing them to jump from a height of 4.5 m. Inger (1966) obtained comparable data for three species of *Rhacophorus* from Borneo that were forced to jump from a height of 5.4 m and Cott (1926) recorded results of a high tower test of the Neotropical hylid, *Phrynohyas venulosa*. Table 1 compares these results with ours. *A. spurrelli* does not parachute as well as *R. nigropalmatus*, the best known anuran parachutist (Saville, 1962) but, allowing for animal size and a lower release

height, it performed almost as well as *R. nigropalmatus* and *R. otitophus* in terms of horizontal distance from the release point. *Agalychnis* has forefeet and hindfeet almost fully spread. It has a hind foot area comparable to those of the two species of *Rhacophorus* just mentioned. It lacks the fringes found on the limbs of many *Rhacophorus* and large neotropical hylids such as *Hyla miliaria*.

There is no doubt that *A. spurrelli* is a parachuting frog as defined by Oliver (1951) in his review of aerial activity in amphibians and reptiles. He suggests that one criterion that can be applied to all gliders and parachutists is the rigid, immobile posture with outspread limbs that is adopted during the "flight." Cott (1926) and Ripley (1964) have illustrations of this posture in *Phrynohyas venulosa* and *Rhacophorus nigropalmatus*. Non-performers such as *Rana temporaria* and *Hyla arborea*, have no control and tend to wriggle and fall end over end (Cott, 1926). Parachuting *A. spurrelli* adopted a posture similar to that described by Inger (1956) for *Rhacophorus pardalis* with the spread feet held slightly above the plane of the body.

"Flying" frogs were first mentioned by Wallace (1869, p. 49) with reference to *Rhacophorus nigropalmatus*. Oliver (1951) suggested that frogs could only parachute, which was defined by an angle of descent of less than 45 degrees from the vertical. Inger (1956, 1966) clearly describes the postural criteria necessary to parachuting in four species of *Rhacophorus* and his last trial for *R. nigropalmatus* shows true gliding, since the glide angle was greater than 45 degrees (Table 1). Duellman (1970) described what may be gliding in *Hyla miliaria* and Cott (1926) demonstrated parachuting in the South American hylid *Phrynohyas venulosa*. In addition to *A. spurrelli*, we observed parachuting posture in two *A. callidryas* and one *Hyla Boulengeri*.

Hendrickson (in Saville, 1962) stated that *R. nigropalmatus* has little power of steering. The *Agalychnis* tested by us showed good control in most tests. If the frog was well settled and oriented before take off, it could land as much as 35 degrees to the right or left and facing 180 degrees from its original direction of flight. The larger females seemed to have better control. They would drop about 2.5 m before making an adjustment that usually brought them back towards the building from where they were released. One frog changed her direction twice in one jump.

TABLE 1. Results of jumping tests and total hind foot area of three species of *Rhacophorus*, *Phrynohyas venulosa*, and *Agalychnis spurrelli*. *Rhacophorus* data from Inger (1966) except 65mm; *R. nigropalmatus* data from Gadow (1901, p. 247); and *Phrynohyas* data from Cott (1926).

Snout-vent (mm)	Area of two hind feet (cm ²)	Height of release (m)	Horizontal length of jump (m)
<i>Rhacophorus otitophus</i>			
86	5.3	5.4	4.0
same animal	—	5.4	3.0
72	3.9	5.4	3.7
<i>Rhacophorus pardalis</i>			
43	3.8	5.4	3.2
same animal	—	5.4	3.2
42	3.8	5.4	2.5
<i>Rhacophorus nigropalmatus</i>			
89	22.1	5.4	4.8
same animal	—	5.4	5.0
same animal	—	5.4	7.3
65	12.0	—	—
<i>Phrynohyas venulosa</i>			
—	—	42.7	27.4
<i>Agalychnis spurrelli</i>			
46-67	—	4.5	1.5-4.0
median 50*	—	—	median 2.2
49	2.6	—	—
49	2.8	—	—
59	4.2	—	—
66	5.4	—	—

* Composite of 31 trials.

Saville (1962) suggested that parachuting and gliding can perform three functions in vertebrates: prevention of injury, escape from predators, and pursuit of prey. All of the known parachuting species of frogs are highly arboreal, and prevention of injury and escape from predators probably are important factors selecting for this behavior and the morphological adaptations which make it more effective. In addition, parachuting and gliding would seem to be helpful in arboreal habitats, where the discontinuous substrate encourages some sort of aerial locomotion.

EVOLUTIONARY CONSIDERATIONS

It is not possible to say for certain whether the massive breeding aggregation of *Agalychnis spur-*

relli which we witnessed is a regular, or even frequent, occurrence at "Caiman Pond". However, the unusually favorable nature of the conditions at the breeding site and the extremely large number of participating frogs suggest that such may be the case. This possibility gives rise to the following speculations, which may serve as a stimulus for further observation and thought, concerning the possible significance of some aspects of what we have reported.

Leaf-scraping by male *A. spurrelli* (as seen at this site) may have evolved as a direct method of removing eggs from the leaves used for breeding. Presumably males would have a higher probability of removing eggs fertilized by other males than they would of destroying their own. On the other hand, leaf-scraping may have evolved as a mechanism for cleaning epiphyllic plants from the leaf surfaces. Epiphyllic plants, especially leafy liverworts, are very common on the Osa Peninsula and many of the leaves in the egg-laying area were partially covered. However, all the leaf-scraping that we observed was carried on by males on egg-covered leaves.

With density-dependent mortality factors concentrated during the time of the breeding chorus and egg-laying, selection might well favor frogs that breed before or, especially, slightly after the majority. By the time the observed aggregation had dissipated, a large proportion of the earliest egg masses had been scraped off of the leaves. This factor alone would provide strong selection for the eggs of the females that laid last. Weather factors, such as the onset of the dry season, might ultimately determine the magnitude of the shift towards later breeding, but there is plenty of leeway on the Osa since the rains are heavy and dependable until late October. The presence of recently hatched tadpoles under the breeding trees may indicate that selection has already started to isolate smaller breeding groups from the main aggregation. Evidently all of the previous spawning was hatched before the first eggs were laid in the giant aggregation.

Another possible consequence of the density of tadpoles produced by the apparently high survival rate in the instance we observed may be stunting (Rose, 1960). This could conceivably be an explanation for the small size of adult frogs from Osa, as noted above. Unfortunately, Duellman (1970) gives measurements for tadpoles of *A. spurrelli* only from the Osa Peninsula, so useful comparative data are not available at this time.

CONCLUSIONS

Wide variation in survival rates of different sections of the life cycle may be characteristic of frog populations, especially those that ordinarily breed in temporary ponds. In these species, selection for high reproductive potential (the *r*-selection of MacArthur and Wilson, 1967, p. 149) is most important since the ephemeral habitat and fluctuating environment selects species with high reproductive rates and the ability to recover from catastrophic losses. It is little wonder that temporary pond breeders such as *A. spurrelli* and *S. baudini* (Gadow, 1908), under short-term, benign conditions, can flood the habitat with young frogs. Our observations suggest that short-term fluctuations may be necessary in order to maintain long-term stability (see also Preston, 1969).

Evidence, fortified by the present observations, is continuing to accumulate (Lloyd *et al.*, 1968; Preston, 1969; Smith, 1970) that tropical populations are not especially constant. Environmental parameters and perturbations must be weighted with respect to a species' ecology rather than against some general concept of "stability" that is supposedly unique to tropical systems.

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HERMIT CRABS FROM THE TROPICAL EASTERN PACIFIC

I. DISTRIBUTION, COLOR, AND NATURAL HISTORY OF SOME COMMON SHALLOW-WATER SPECIES

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ABSTRACT: Observations on distribution, natural history, and color in life are presented for 12 species of hermit crabs (Diogenidae and Paguridae) collected from the intertidal and shallow subtidal between Paíta, Perú and Bahía de la Magdalena, Baja California, México.

The present paper is based on hermit crabs collected by the first author from April to June 1968 during Stanford Oceanographic Expedition 18 aboard R/V "Te Vega." The expedition, under the leadership of Donald Abbott, sampled the intertidal and shallow water subtidal from Paíta, Perú to Bahía de la Magdalena, Baja California, México. This area covers the entire tropical region of the Eastern Pacific (Panamic faunal province) with the exception of Golfo de California and various offshore islands; it also includes the extreme northern portion of the southern warm-temperate region (Peruvian faunal province), an overlap area within which many tropical animals reach the southern limit of their distribution. A map showing the collecting stations of the expedition, and a station list, are presented in figure 1 and table 1, respectively.

During the expedition special attention was paid to the biology of the hermit crabs collected and to their colors in life. Although the literature on hermit crabs of the tropical Eastern Pacific is fairly extensive, few papers have been published dealing with the natural history of pagurids from this area. Furthermore, very little information has been available on the color of living hermit crabs from the tropical Eastern Pacific; almost all the systematic work has been done on material with its color lost or changed subsequent to preservation. Since color and color pattern often provide one of the easiest ways to distinguish hermit crabs in the field, the lack of such information can make the work of the field biologist much more difficult. Data on color in life also frequently provide a very useful tool to the systematist for the initial separation of species that are difficult to distinguish on morphological grounds alone.

Twenty-seven species of hermit crabs were collected during the expedition. Originally, the

objective of our study was to set forth the information obtained on their color and biology, otherwise merely enumerating the species with a few pertinent references and data on collecting localities and general distribution. However, the collection proved to include several new and little-known species of *Paguristes* and *Pagurus* which, for practical reasons, are best treated separately; they will be the subject of two additional papers (Haig and Ball, in preparation). Data on *Coenobita compressus* have been published elsewhere (Ball, 1972). The remaining 12 species, which are the subject of this first part of our study, include many of those most commonly encountered in shallow water within the geographical area covered. This paper is contribution No. 349 from the Allan Hancock Foundation.

METHODS

Collections were made intertidally and by SCUBA diving; an otter trawl was used at station 20c. The most efficient method found for removing the animals from their shells was to add a small amount of magnesium chloride ($MgCl_2$) to the seawater covering them and then allow them to asphyxiate. Their usual response to low oxygen levels was to at least partially leave the shell, and thus their removal was greatly facilitated. Color descriptions and color photographs were made as soon as possible after the animals were removed from their shells.

Feeding was studied by field observation and

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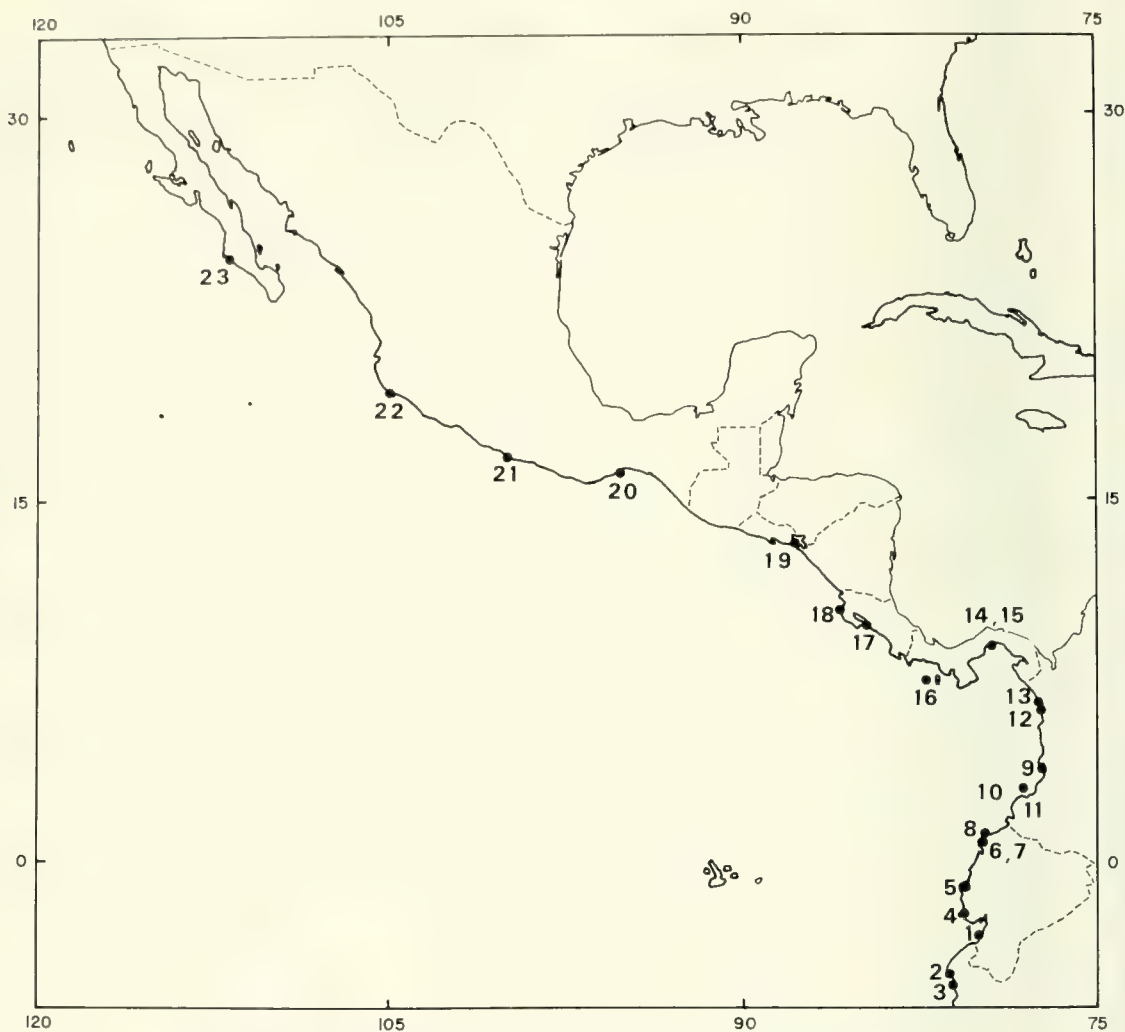


Figure 1. Collecting stations of Stanford Oceanographic Expedition 18.

by examination of gut contents. Intertidal species which were to be used in feeding studies were fixed immediately in the field. Specimens obtained by SCUBA diving were fixed as soon as possible, but in some cases up to six hours elapsed between collection and fixation.

Following the termination of the cruise, the collections were taken to the Allan Hancock Foundation where final determinations were made by the second author. The crabs are housed in the Allan Hancock Foundation.

Measurements given in this report refer to carapace length. References given with each species are to original descriptions; papers giving good illustrations and information on color and biology; and recent papers citing extensions of range. Our authority for the spelling of Spanish

place-names is *Index to Map of Hispanic America* ("Millionth Map") (U.S. Government Printing Office, 1945).

SPECIES COLLECTED FAMILY COENOBITIDAE

Coenobita compressus H. Milne-Edwards

Cenobita compressa H. Milne-Edwards, 1837:241.

Cenobita intermedia Streets, 1871:241.

Cenobita panamensis Streets, 1871:241.

Coenobita compressus: Boone, 1931:145, text-fig. 3; Glassell, 1937:242; Holthuis, 1954:16, text-figs. 4a,b; Bright, 1966:188, 189, text-figs. 4A-C; Haig, Hopkins, and Scanland, 1970:15, 27; Ball, 1972: 265 *et seq.*

TABLE 1. Station Data, Stanford Oceanographic Expedition 11

STATION	LOCALITY	DATE (1968)	POSITION
1	Isla de Santa Clara, Golfo de Guayaquil, Ecuador	5-7 Apr	3°10'S—80°00'W
2	Talara, Perú	8-9 Apr	4°34'S—81°15'W
3	Paita, Perú	10-13 Apr	5°05'S—81°10'W
4	Salinas and vicinity, Ecuador	15-18 Apr	2°11'S—80°59'W
5	Manta, Ecuador	19-20 Apr	0°56'S—80°47'W
6	Punta Galera, Ecuador	22 Apr	0°50'N—80°01'W
7	Punta Sua, Ecuador	23 Apr	0°52'N—79°55'W
8	Atacames Reef, Ecuador	23 Apr	1°00'N—79°43'W
9	Punta Barca, Bahía de Buenaventura, Colombia	26 Apr	3°50'N—77°16'W
10	Punta Mono, Isla Gorgona, Colombia	27 Apr	2°57'N—78°12'W
11	Straits between Islas Gorgona and Gorgonilla, Colombia	28 Apr	2°56'N—78°13'W
12	Bahía de Solano, Colombia	30 Apr-1 May	
	a. Punta San Francisco Solano		6°18'N—77°29'W
	b. Punta Cotudo		6°16.4'N—77°26'W
	c. Punta Nabugá		6°22.8'N—77°23.7'W
	d. Muntas		
13	Bahía de Cupica, Colombia	2 May	
	a. Punta Cruces		6°39.3'N—77°30.6'W
	b. Bahía Chicocoro		6°41'N—77°24.5'W
14	Balboa, Canal Zone and Panama City, Panamá	5-6 May	
	a. Islas Naos and Culebra, Canal Zone		8°54.8'N—79°31.9'W
	b. Punta Paitilla, Panama City		8°58.1'N—79°31'W
15	Isla Taboguilla, Bahía de Panamá, Panamá	7 May	8°48'N—79°31'W
16	Isla Montuosa, Panamá	9 May	7°28'N—82°14'W
17	Area of Islas Negritos and Cedro, Golfo de Nicoya, Costa Rica	11-12 May	
	a. Isla Negrito-adentro		9°49'N—84°52'W
	b. Isla Cedro		9°50.5'N—84°52.2'W
	c. Puntarenas		9°59'N—84°50'W
18	Bahía Brasilito, Costa Rica	13 May	10°25'N—85°49'W
19	Punta Chiquirin and vicinity, Golfo de Fonseca, El Salvador	15-16 May	
	a. La Unión		13°20'N—87°50'W
	b. Punta Chiquirin		13°18'N—87°47'W
	c. Isla Chuchito		13°19.2'N—87°45.6'W
20	Salina Cruz and vicinity, Oaxaca, México	20-22 May	
	a. Bahía Ventosa		16°10.1'N—95°09'W
	b. Salina Cruz harbor		16°9.5'N—95°12.6'W
	c. Tartar Shoals		16°18.8'N—98°39'W
21	Acapulco and vicinity, Guerrero, México	23-24 May	16°50'N—99°55'W
22	Bahía Tenacatita, Jalisco, México	27 May	19°17'N—104°50'W
23	Bahía de la Magdalena, Baja California, México	2 Jun	24°24'N—112°04'W

Remarks: Specimens of *Coenobita compressus* collected and observed during Stanford Oceanographic Expedition 18 were the subject of a separate report (Ball, 1972).

Distribution: Several Chilean records, Estrecho de Magallanes and northward, require confirmation. Paita, Perú, to Santa Rosalía, Golfo de California, México; Bahía de la Magdalena on the outer Baja California peninsula; offshore islands including Galápagos, Isla del Coco, and Revillagigedos.

FAMILY DIOGENIDAE

Dardanus sinistripes (Stimpson)

Pagurus sinistripes Stimpson, 1859:82.

Dardanus sinistripes: Rathbun, 1910:556, 597, pl. 49, fig. 2; Glassell, 1937:251; Haig, Hopkins, and Scanland, 1970:16, 27.

Dardanus imbricatus Rathbun, 1910:556, 597, pl. 49, fig. 3.

Dardanus peruensis Balss, 1921:21.

Localities: Paíta (sta. 3); Punta Galera (sta. 6); off Isla Gorgona (sta. 11); Punta Cotudo (sta. 12b); Isla Taboguilla (sta. 15); Bahía Brasilito (sta. 18); Salina Cruz (sta. 20b); Tartar Shoals (sta. 20c); El Morro and NE corner of La Roqueta, Bahía de Acapulco (sta. 21); La Manzanilla, Bahía Tenacatita (sta. 22); Bahía de la Magdalena (sta. 23).

Measurements: Males 6.1 to 22.7 mm, females 8.8 to 29.0 mm.

Color description: Carapace varies from mottled salmon to tan. Eyestalks salmon, with a tuft of white setae just proximal to golden cornea; ventral side of stalk white, sometimes with two salmon-colored bands. Antennules white to light tan. Antennae uniform pale salmon. Chelipeds red with purplish tones and many purplish tubercles; merus with a dark red band distally; smaller cheliped with coarse red and white hairs. Cutting edge of fingers white, with a narrow longitudinal line of red. Walking legs salmon or mottled salmon and white, with scattered purple tubercles; merus and carpus paler than the two distal segments. Second left walking leg with transverse ridges of purple crossing flattened surface of propodus and dactyl.

Distribution: Bahía de Sechura, Perú, to Isla Tiburón, Golfo de California, México; outer Baja California peninsula as far north as Boca de Santo Domingo. Distribution for this species is subject to revision, however, since there is evidence that two closely related forms have been confused under the name *D. sinistripes* (Biffar and Provenzano, 1972: 799–800).

Natural history: This species is widely distributed both geographically and vertically. During Stanford Oceanographic Expedition 18 it was found in the littoral and to depths of 100 feet, usually on bottoms which were a mixture of sand and gravel. It may be locally very abundant (e.g., at sta. 18). The shells inhabited by this species are often enormous in relation to the size of the crab and it is sometimes difficult to imagine how the crab manages to move its shell. A variety of shells are occupied, although at depths greater than 50 feet there appears to be considerable uniformity in the type of shell occupied at a given locality. Commensal anemones were frequently present on the shell (stas. 15, 18, 20c, 21, 22). At Bahía de la Magdalena (sta. 23) a small specimen had part of its shell coated with orange sponge, while the shells of three larger animals from the same locality bore a dense growth of a hydroid (*Hydractinia* sp.). This hydroid was in the area of the aperture on all three shells and entirely covered one of them. The zooids near the aperture are continuously moved around in the crab's respiratory current when the crab is withdrawn; this would presumably make the

aperture a favorable place for the hydroid to grow. A large polynoid worm was living in one of the shells from sta. 23, and a porcelain crab, *Porcellana paguriconviva* Glassell, was living in the shell with a hermit from sta. 22.

Petrochirus californiensis Bouvier

Petrochirus californiensis Bouvier, 1895:6; Glassell, 1937:251; Steinbeck and Ricketts, 1941:454, pl. 12 fig. 1; Haig, Hopkins, and Scanland, 1970:25, 27; del Solar, Blancas, and Mayta, 1970:24.

Petrochirus granulatus californiensis: Bott, 1955:53, pl. 5 figs. 7a,b.

Localities: Isla Taboguilla (sta. 15); Isla Cedro (sta. 17b); Bahía Brasilito (sta. 18).

Measurements: Males 23.8 and 29.5 mm, females 31.8 mm.

Color description: Carapace pale, with a dark reticulate pattern. Eyestalks uniform reddish-brown with a hint of purple; distally a dark brown chevron, and a white band just proximal to the dark cornea. Antennules white with a longitudinal brown stripe laterally and mesially; brown at the base of the flagellar setae. Antennal flagella alternately banded brown and white, usually three to five brown segments alternating with three to five white segments. Chelipeds reddish-purple; cutting edge and tip of fingers white; mesial surface of both meri with two large maculations of deep purplish-brown at distal end, lateral surface with one such blotch at lower distal corner. Dactyl of walking legs dark reddish-brown, with abundant reddish-brown hairs on margins. Other segments of walking legs pale reddish-purple; merus with a large maculation of dark purplish-brown midway along dorsal margin.

Distribution: Caleta La Cruz, Perú, to Punta Peñasco, Golfo de California, México; north to Bahía de Santa María on the outer Baja California peninsula.

Natural history: This species was found on bottoms of sand and gravel to a depth of 35 feet. It often carries a number of commensals within its shell. For example, one individual from sta. 15 with a carapace length of 31.8 mm, living in a shell of *Vasum cestus* (Broderip), shared it with two pairs of porcelain crabs, *Porcellana cancrisocialis* Glassell; a number of polychaetes; and several red polyclad flatworms, *Emprostopharynx opisthophorus* Bock, ranging up to 20 mm in length. On the outside of the shell were barnacles, bryozoans, and algae. In the shell with a 23.8 mm *Petrochirus* from sta. 17b were two juvenile porcelain crabs, *Porcellana paguriconviva* Glassell, and a polyclad flatworm, *Stylochus* sp. A specimen from sta. 18 bore several large commensal anemones on its shell.

Aniculus elegans Stimpson

Aniculus elegans Stimpson, 1859:83; Boone, 1931: 140, text-fig. 1; Walton, 1950:192; Haig, Hopkins, and Scanland, 1970:16, 27.

Aniculus longitarsis Streets, 1871:240.

Localities: Salinas off Punta Mandinga (sta. 4); Manta (sta. 5); Atacames Reef (sta. 8); Punta Barca (sta. 9); Punta Cotudo (sta. 12b); Isla Taboguilla (sta. 15); Isla Naos (sta. 14a); Punta Paitilla (sta. 14b); Bahía Brasilito (sta. 18); Tartar Shoals (sta. 20c); Bahía de la Magdalena (sta. 23).

Measurements: Males 19.9 to 51.1 mm, non-ovigerous females 20.7 to 35.1 mm, ovigerous female 31.4 mm.

Color description: Carapace shield with distinct grooves marking the various areas; protogastric and branchial areas deep red, others pink. Posterior carapace deep red with white splotches. Eyestalks uniform light tan; corneas dark brown. Eyescales reddish. Antennules uniform tan. Antennae uniform reddish-brown. Chelipeds mottled red and pink; transverse rings bordered with a fine red line and with a fringe of fine white hairs along their distal edge. Fingers with small, black, corneous spinules and tufts of coarse, dark red, white-tipped hairs. Walking legs mottled red and pink, dactyl red, propodus with a subdistal red band; transverse rings bordered with a fine red line and with long, red, white-tipped hairs.

Distribution: Cabo de San Francisco, Ecuador, to Golfo de California, México (no precise locality in the Gulf has been specified, but the species occurs there at least as far north as Bahía de San Carlos); north to Bahía de la Magdalena on the outer Baja California peninsula. The known range is now extended southward in Ecuador from Cabo de San Francisco to Punta Mandinga.

Natural history: This species was collected by dredging in 13 fathoms (24 m) and by diving to depths of 35 feet, on a variety of substrates including sand and gravel, mixed rock and sand, rocky outcrops, and *Pocillopora* coral. Several times these animals were found clustered together in groups of two or three. The crab is frequently very small in proportion to the size of shell it occupies. Gut contents of three specimens from stas. 14a and 14b were examined and found to include unidentifiable organic matter and parts of a small crustacean. A 51.1 mm specimen from Isla Taboguilla had a pair of commensal porcelain crabs, *Porcellana paguriconviva* Glassell, and a 35.1 mm specimen from Bahía de la Magdalena harbored one crab of the same species.

Trizopagurus magnificus (Bouvier)

Clibanarius magnificus Bouvier, 1898:378.

Clibanarius cheyrkini Boone, 1932:29, text-fig. 8.

Trizopagurus magnificus: Forest, 1911: 17, figs. 2, 11, 18; Haig, Hopkins, and Scanland, 1970:17, 27.

Localities: Manta (sta. 5); Punta Cotudo (sta. 12b); Isla Montuosa (sta. 16); Isla Taboguilla (sta. 15); Isla Naos (sta. 14a); Isla Neerito (sta. 14a); Bahía Brasilito (sta. 18); El Morro, Bahía de la Magdalena (sta. 21); Bahía de la Magdalena (sta. 23).

Measurements: Males 8.0 to 20.8 mm, non-ovigerous females 6.3 to 15.2 mm, ovigerous female 6.4 to 17.1 mm.

Color description: Shield brown with white spot posterior part of carapace salmon with white spot. Eyestalks brown with white spots; cornea red. Proximal segment of antennules brown with white spot; distal segment and flagellum uniform bright orange. Antennae bright orange. Chelipeds brown with large white tubercles; cutting edge of fingers black. Walking legs brown with large spots varying from white to bright orange.

Distribution: Isla de la Plata, Ecuador, to Golfo de California, México (apparently the southernmost part only); north to Bahía de la Magdalena on the outer Baja California peninsula; Archipiélago de Galápagos.

Natural history: *Trizopagurus* was found mainly on rocky outcrops and on living heads of *Pocillopora* coral, from the intertidal zone to 30 feet. They seemed rather gregarious, with groups of seven or eight frequently observed. The crabs were sometimes so tightly wedged among the *Pocillopora* branches that it was very difficult to imagine how they were able to move. They occurred in a variety of shell types.

At sta. 14a several *Trizopagurus* were observed feeding by scraping at the rocks with both chelipeds. They appeared to be eating fine algae. Gut contents of 11 individuals from five localities included coarse sand and shell fragments, unidentifiable fine organic matter and small pieces of algae, two of which appeared to be *Gelidium pusillum* (sta. 12b) and *Polysiphonia* sp. (sta. 21).

Clibanarius panamensis Stimpson

Clibanarius panamensis Stimpson, 1859:84; Steinbeck and Ricketts, 1941:454, pl. 16 fig. 1; Holthuis, 1954:23, text-figs. 7, 8; Bott, 1955:53, pl. 5 figs. 6a,b; Haig, Hopkins, and Scanland, 1970:17, 27.

Localities: Punta Barca (sta. 9); Muntas (sta. 12d); Isla Chuchito (sta. 19c).

Measurements: Males 11.0 to 22.8 mm, non-ovigerous females 11.5 to 17.3 mm, ovigerous female 11.9 mm.

Color description: Carapace mottled olive drab and white. Eyestalks uniform light tan with hints of green. Antennules olive drab; flagellum with a longitudinal stripe of bright orange at base of setae.

Antennae uniform olive drab. Chelipeds brown with longitudinal orange stripes; manus and fingers covered with white tubercles. Ground color of walking legs dark brown, with stripes, varying in color from orange to white, running the entire length of each segment; outer surface with four or five light stripes on merus, four on carpus, propodus, and dactyl. On the propodus the dark and light stripes are subequal in width.

Distribution: Isla de la Correa near Capón, Perú, to Santa Rosalía, Golfo de California, México; north to Bahía de Santa María on the outer Baja California peninsula.

Natural history: This species was found intertidally on fine sediment in protected areas. At Punta Barca several crabs were observed on the bottom of an intertidal stream, moving their chelipeds rapidly back and forth over the sandy bottom while apparently feeding. Periodically a cloud of particles was shot out anteriorly. The gut of one of these animals was packed solidly with mud and fine organic matter cementing some larger particles of sand. A few small fragments of algae were present.

Clibanarius albidigitus Nobili

Clibanarius albidigitus Nobili, 1901:24; Holthuis, 1954:25, text-fig. 9; del Solar, Blancas, and Mayta, 1970:23.

Localities: Paita (sta. 3); Isla de Santa Clara (sta. 1); Punta Brava near Punta Mandinga (sta. 4); Manta and nearby Punta Mal Paso (sta. 5); Punta Galera (sta. 6); between Islas Gorgona and Gorgonilla (sta. 11); Punta Mono (sta. 10); Punta Barca (sta. 9); Isla Montuosa (sta. 16); Isla Taboguilla (sta. 15); Punta Paitilla (sta. 14b); Isla Chuchito (sta. 19c).

Measurements: Males 3.2 to 10.8 mm, non-ovigerous females 3.5 to 7.5 mm, ovigerous females 3.1 to 7.1 mm.

Color description: Carapace mottled olive drab and tan. Eyestalks olive drab, cornea black. Antennular peduncles olive drab, flagellum orange. Antennae orange. Chelipeds olive drab with white tubercles. Walking legs olive drab with white tubercles; outer and inner sides of dactyls white.

Holthuis (1954:27), describing the color of specimens from El Salvador, noted that they had a longitudinal white stripe on the propodus, carpus, and merus of the walking legs (fig. 9c) in addition to the characteristic broad, longitudinal white stripe on the dactyl. He added that in adults the white stripe was often lacking on the propodus, carpus, and merus (fig. 9b). In a series of more than 20 specimens from El Salvador collected during Stanford Oceanographic Expedition 18, the situation is exactly as described and illustrated by Holthuis, with most, although not all, of the crabs longitudinally striped

with white on all four segments. On the other hand, specimens collected further south, almost without exception, have only the very characteristic broad white stripe on the dactyl and no trace of it on any other segments of the walking legs. In a series of 56 specimens from Punta Paitilla a few very small individuals show some lack of dark pigment on the propodus.

Distribution: Caleta La Cruz, Perú (del Solar, Blancas, and Mayta, 1970; other records listed by these authors are in error) to La Libertad, El Salvador. The known range is now extended southward in Perú from Caleta La Cruz to Paita.

Natural history: This species appears to be highly adaptable, being found higher in the intertidal than any other of the marine hermits encountered, and existing over a considerable range of temperatures. It is typically found in rocky tidepools and seems to be especially abundant on rocky intertidal flats. A wide variety of mollusk shells is occupied at various localities. *Calcinus obscurus* Stimpson is usually found in the same environment, although its distribution is centered slightly lower in the intertidal; within the area of overlap the two species are usually found grouped together. At times when the *Clibanarius* are inactive they form piles consisting of up to a few hundred individuals under rocks or out in the open. Feeding is done by scraping at the surface of rocks with the chelipeds. Gut contents of 35 specimens from six localities were examined. In almost all cases the gut was packed with fine sediment and algal fragments (*Bostrychia radicans* being the only identifiable alga); diatom frustules and one copepod exoskeleton were also found. In the field this species was seen feeding on *Enteromorpha* and on *Padina* or something encrusting it.

Clibanarius digueti Bouvier

Clibanarius digueti Bouvier, 1898:379.

Locality: Bahía de la Magdalena (sta. 23).

Measurements: Male 10.0 mm, ovigerous female 8.5 mm.

Color description: Carapace mottled tan. Eyestalks olive drab to dark green; cornea with white spots on a dark background. Antennules olive drab to dark green, with bright orange flagellum. Antennal peduncles red, flagellum orange. Chelipeds brown with abundant bluish-white tubercles; fingers orange. Walking legs brown with many white spots; dactyl reddish-orange distally, shading to brown at base of segment.

Distribution: Throughout Golfo de California, México. It is now recorded for the first time from the outer side of the Baja California peninsula.

Habitat: This species was found in rocky pools in the lower intertidal.

Calcinus obscurus Stimpson

Calcinus obscurus Stimpson, 1859:83; Nobili, 1901:26; Holthuis, 1954:20, text-figs. 5, 6.

Localities: Isla de Santa Clara (sta. 1); Salinas and vicinity (sta. 4); Punta Galera (sta. 6); between Islas Gorgona and Gorgonilla (sta. 11); Punta Mono (sta. 10); Punta Barca (sta. 9); Punta San Francisco Solano (sta. 12a); Punta Cruces (sta. 13a); Isla Montuosa (sta. 16); Isla Taboguilla (sta. 15); Isla Naos (sta. 14a); Punta Paitilla (sta. 14b); Isla Negrito (sta. 17a); Bahía Brasilito (sta. 18); Punta Chiquirin (sta. 19b).

Measurements: Males to 18.0 mm, non-ovigerous females to 14.0 mm, ovigerous females 5.6 to 10.8 mm.

Color description: Carapace shield olive green with punctae varying from light blue to white. Posterior carapace tan and white. Eyestalks olive green with a broad white ring just proximal to black cornea. Eyescales orange. Antennules olive green proximally; distal segment of peduncle and flagellum orange. Antennae uniform bright orange. Chelipeds olive drab; margins orange; cutting edge of fingers white. Walking legs vary from olive drab to brown, with whitish punctae; dactyl with a distal orange patch at base of nail and often with varying amounts of orange subproximally (in small specimens the dactyl generally has a proportionately greater area of orange than in large individuals).

Distribution: Bahía de Santa Elena, Ecuador, to La Libertad, El Salvador.

Natural history: This species is widely distributed and often very abundant in the lower intertidal. Its intertidal distribution overlaps that of *Clibanarius albidigitus*, and the food and habitat requirements of the two species appear quite similar. Many types of mollusk shells are occupied by *Calcinus obscurus*.

At several stations (especially 9 and 10) many large *C. obscurus* were out on the upper surface of rocks with the aperture of the shell facing upward and the crab withdrawn inside. Reese (1969:349, text-fig. 3A,B) reported similar behavior for *Calcinus laevis* (Randall) and *Clibanarius corallinus* (H. Milne-Edwards) at Eniwetok Atoll, Marshall Islands.

Feeding usually appears to involve scraping fine algae and detritus from the rocks. Most of the work is done by the small right cheliped while the much larger left cheliped is used mainly as a support. These crabs were observed feeding on *Padina* or the material encrusting it (sta. 1), and on *Gelidium pusillum* (sta. 12a).

Gut contents of 23 crabs from 1 were examined. Most of the gut was packed with fine sand and unidentifiable matter with some recognizable algal fragments. Identifiable material included *Monostroma adoreanum* (sta. 1), *Gelidium* sp. (sta. 1), and what appeared to be fragments of small crustaceans (stas. 1 and 4).

Calcinus californiensis Bouvier

Calcinus californiensis Bouvier, 1898:380; Glassell 1937:252; Haig, Hopkins, and Scanland, 1970:1627.

?*Calcinus californiensis*: Chace, 1962:627, text-figs. 5, 6.

Localities: NE corner of Isla Roqueta, SW of Bahía de Acapulco (sta. 21); La Manzanilla, Bahía de Tenacatita (sta. 22); Bahía de la Magdalena (sta. 23).

Measurements: Males 4.2 to 13.7 mm, non-ovigerous females to 11.4 mm, ovigerous female 4.2 mm.

Color description: Carapace shield olive drab with bluish punctae and orange margins. Posterior carapace mostly white. Eyestalks olive drab with a broad white ring just proximal to black cornea. Eyescales white. Antennules olive drab proximally; distal segment of peduncle and flagellum orange. Antennae reddish-orange. Chelipeds olive drab with bluish punctae; margins reddish-orange; cutting edge of fingers white. Walking legs bright reddish-orange; dactyl solid reddish-orange, without rings or patches of another color; merus of first walking legs with a large olive spot laterally.

Distribution: México: Acapulco to Isla San José, Golfo de California, and to Bahía de la Magdalena, west coast of Baja California; Isla Clipperton.

Habitat: This species was found on boulders interspersed with sand, from the lower intertidal to a depth of approximately 10 feet.

Isocheles, sp. indet.

Localities: Salinas at Punta Mandinga (sta. 4); near Puntarenas (sta. 17c).

Measurements: Males 12.0 and 12.8 mm (sta. 4); male 8.2 mm, females 6.5 and 10.0 mm (sta. 17c).

Color description: Carapace shield mottled brown and white. Eyestalks white with two longitudinal brown stripes, one dorsal and the other mesal; cornea black. Antennules white with two longitudinal brown stripes, one dorsal and the other ventral, on the distal segment of the peduncle. Antennae flagella with a greenish band on each segment. Merus of chelipeds mottled brown and white, carpus white with broad elongate areas of brown, dactyl reddish-brown. Merus and carpus of walking legs brown.

propodus brown dorsally and white ventrally, dactyl brown and white.

The above notes were taken on specimens from Punta Mandinga. The color and markings of the individuals from Puntarenas are much the same, with the following exceptions: the longitudinal stripes on the eyestalks appear black instead of brown; the walking legs are tan with some green, and there is a broad white band at the distal end of the propodus and a little white at the proximal end of the dactyl.

Habitat: Low intertidal, sand and scattered rocks (sta. 4). At the water's edge on a gently sloping sandy beach, low in the intertidal (sta. 17c).

Remarks: Three species of *Isocheles* are currently recognized from the eastern Pacific, and still others are to be described by J. Forest of the Muséum National d'Histoire Naturelle (Paris), who is revising the genus (Forest and Saint Laurent, 1968:107). Until this revision is completed the status of the "Te Vega" specimens must remain uncertain.

Paguristes spp.

Paguristes perrieri Bouvier, *P. anahuacus* Glassell, and five undescribed species of this genus were collected during Stanford Oceanographic Expedition 18. These will be treated in the second part of the present study.

FAMILY PAGURIDAE

Pagurus perlatus H. Milne-Edwards

Pagurus perlatus H. Milne-Edwards, 1848:60; Haig, 1955:18, 21, text-figs. 3, 4; Haig, 1968:21; del Solar, 1970:46 [*Pagurus*].

Bernhardus obesocarpus Dana, 1852:445; Dana, 1855: pl. 27 figs. 5a-d.

Locality: Paita Harbor (sta. 3).

Measurements: Small male 5.5 mm.

Color description: Carapace mottled reddish-brown and white. Eyestalks olive with fine yellow spots; cornea brown with gold flecks. Antennules with yellow spots on a transparent background; a large, dark green spot on distal part of terminal segment of peduncle, and a similar spot on flagellum. Antennal scale and peduncle with fine yellow spots on a tan background; flagellum irregularly ringed, usually with three brown segments alternating with a white segment. Proximal articles of chelipeds mottled brown and white; chela mostly white with some tan. Merus and carpus of walking legs mottled tan and white, changing to mostly white on propodus; dactyl white.

Distribution: Puerto Corral, Chile, to department

of Tumbes, Perú. Unlike the other hermit crabs treated in this paper, *Pagurus perlatus* is a warm-temperate rather than tropical species.

Habitat: This species was collected on a bottom of fine sand at a depth of approximately 10 feet.

Pagurus spp. (*miamensis* group)

Forest and Saint Laurent (1968:116) designated as the "*miamensis* group" a number of species of *Pagurus* with close affinities to *P. miamensis* Provenzano of the tropical West Atlantic. Seven species belonging to this group were collected during Stanford Oceanographic Expedition 18: *Pagurus lepidus* (Bouvier), *P. benedicti* (Bouvier), *P. galapagensis* (Boone), *P. villosus* Nicolet, and three undescribed species. We shall treat these forms in the third part of the present study.

Pylopagurus varians (Benedict)

Eupagurus varians Benedict, 1892:24.

Pylopagurus varians: Glassell, 1937:253; Walton, 1954:141, 152, pl. 42 E-H.

"Stag-horn": Smith, 1966:30, 2 text-figs.

Locality: Bahía de la Magdalena (sta. 23).

Measurements: The single specimen, which had been kept alive in an aquarium, was eaten by another aquarium animal before it could be preserved and measured.

Color description: Shield orange; posterior carapace with reddish-brown spots on an orange background. Eyestalks reddish-brown; cornea bright orange. Basal segments of antennules clear, distal segment of peduncle with alternating reddish-brown areas and dorsal white spots; flagellum reddish-brown. Antennal peduncle transparent except acicle, which has alternating transverse bands of white and reddish-brown; flagellum with three to five reddish-brown segments alternating with a white segment. Merus of large cheliped mottled red and white, carpus pink with a few deep red tubercles, chela reddish-brown to orange. Merus and chela of small cheliped mottled red and white, carpus with distinct transverse red and white bands. Walking legs mostly reddish-brown with a white area at distal end of each segment.

Distribution: Islas Secas, Panamá, to Bahía de Tepoca on the east side of Golfo de California, México, and Arena Bank to Isla Angel de la Guarda on the west side of the Gulf. It is now recorded for the first time from the outer side of the Baja California peninsula, and also in somewhat shallower water than previously: the recorded bathymetric range is 6 to 100 fathoms (11 to 183 meters).

Natural history: The specimen was taken on a mixed bottom of sand and rock at a depth of approximately 20 feet. The shell of this animal had been covered, and perhaps replaced, by a

white hydrocoral which formed five antler-shaped branches. When turned completely upside down on these branches, the crab seemed to be unable to right itself. The hydrocoral had a number of amphipods associated with it.

The association of *Pylopagurus varians* with a hydrocoral was briefly mentioned by Walton (1954), and also by Glassell (1937) who referred to it as a "bryozoan growth." Smith (1966) discussed the association in more detail and illustrated the crab with its carapace. His specimen from Golfo de California, living with a many-branched hydrocoral, was not mentioned by name but one of us (J. Haig) has seen it and confirmed its identity.

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SYSTEMATICS OF *PTEROCLADIA MEDIA* FROM CALIFORNIA

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ABSTRACT: The finding of unilocular cystocarps on herbarium specimens of *Gelidium crinale* var. *luxurians* from California requires that the plants be referred to the genus *Pterocladia*. *Pterocladia media* Dawson (1958) is expanded for this purpose. *Gelidium sinicola* Gardner (1927) may possibly also belong here. Additional collections of this *Pterocladia* species are noted.

The genus *Pterocladia* J. Agardh (1851) was established for *Gelidium lucidum* (Turn.) Sond. Species in both genera are similar in vegetative morphology. Cystocarps in *Pterocladia* are unilocular and in *Gelidium*, bilocular; a consequence of carposporophyte development from one surface of an axis, or from both. Studies of species referred to these two genera (Fan, 1961; Feldmann and Hamel, 1936; Loomis, 1949; Okamura, 1934) have suggested characters by which non-cystocarpic plants of one genus might be distinguished unequivocally from the other. Some distinctions have proved useful, but often there remain specimens of dubious or tentative assignment. Four assignments involving *Gelidium-Pterocladia* collections from California are discussed here and an inclusive answer proposed.

One such question arose during a study (Stewart, 1968) of the morphological variation relative to the ecology of *Pterocladia* in California. Specimens in certain collections were extremely narrow, and in addition, sparsely branched, compared with more regular pinnate branching and broader axes characteristic of *P. capillacea*. These specimens were set aside for further study and not included in the work on *P. capillacea*. Other collections of the distinctive entity have been made subsequently from several sites on the southern California coast.

Pterocladia media Dawson (1958) was described from a single collection from La Jolla (Dawson, 15609, AHF 63142, 63143, two isotype sheets) and contained no fertile plants. He stated that these small plants differed in "size" from *P. pyramidale* (Gardner) Dawson (= *P. capillacea*). *Pterocladia capillacea* plants 10–20 cm in height are abundant intertidally but even much smaller specimens are regularly branched with the axes mostly as wide as in taller plants. Dawson (pers. comm.) commented that the comparative lack of branching and narrow axes were note-

worthy distinctions between the two species in San Diego. Attempts to locate additional material at the type locality were unsuccessful, and the species apparently was not known from other than the type collection.

Gelidium crinale forma *luxurians* was described (Collins, 1906) from collections made by Mrs. Snyder from San Diego, having been earlier distributed under this name in Collins. Holden, and Setchell, *Phycotheca Boreali-Americana* No. 1138. Gardner (1927) referred some tetrasporangial plants from Santa Monica to this taxon and raised its status from "forma" to "variety." Numerous California collections of small, narrow (thereby appearing terete), sparsely branched gelidiaceous algae have been identified as belonging to this variety. Sexual plants were not known from the Pacific coast. On several Dawson sheets in the Herbarium at Allan Hancock Foundation, there are comments indicating that he wondered whether they might better belong with *Pterocladia* on the basis of vegetative morphology. During a recent study of California *Gelidium*, three specimens attributed to *G. crinale* var. *luxurians* were found to have unilocular cystocarps (Fig. 1). This necessitates referring the collections of this variety, as known from California, to the genus *Pterocladia*.

Another poorly defined taxon is *Gelidium sinicola* Gardner (1927); described on the basis of a single non-fertile collection from San Francisco, UC 276620. Since then the epithet has been applied inconsistently to several different small *Gelidium* spp. Measurement data (Table 1) and general appearance of the type material of *G. sinicola* are similar to data concerning *G. crinale*.

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TABLE 1. Morphological data on *Pterocladia media*, *Gelidium sinicola*, and *Gelidium crinale* var. *luxurians* from California.

	Height in cm	Cross Section in μ m		Branching Pattern	Rhizoidal Filaments	♀	♂	♂
		Basal	Apical					
<i>P. media</i> , as described in Dawson, 1958	to 3	140 broad, 100-140 thick	300-400 × 100-140	pl. 21. Irregular; some more pinnate distal	Scant, inner medulla	-	-	-
"Undet" <i>Pterocladia</i> , JS 641, 1424, 1702	to 5.5	340-120, of uniform dimensions throughout		Irregular; as shown for <i>P. media</i> , Dawson, 1958	Few to abundant in medulla	-	-	+
<i>Gelidium sinicola</i> UC 276620, type specimen	4.5	250 × 240	200 × 180	Irregular, mostly distal. Ultimate branchlets appear almost terete.	Few in outer medulla, seen in a basal section	-	-	-
<i>G. sinicola</i> , as described in Gardner, 1927	4.5- 6	"less than half a mm in diameter"		"Abundant" (this is relative; see pl. 47) and "irregular"	Sparse, among medullary cells	-	-	In pl. 47
<i>G. crinale</i> f. <i>luxurians</i> UC 693170, PBA 1138	7	170 × 100	200 × 120	Few above and below, irregular and various. Ultimate appearing terete	Scarce, central	-	-	-
<i>G. crinale</i> var. <i>luxurians</i> GMS 7458, PBA 1138	6.5	200 × 120	160 × 120	Unbranched or sparsely branched	Scarce, central	-	-	-
<i>G. crinale</i> var. <i>luxurians</i> AHF 69461, 51372, 51368, 4184, 64658, 67919, 68106, 55229, 4185, 64918	2-6	Mostly about 200-300 broad, 100 thick, of uniform dimensions in all axes		Unbranched or branching irregular and sparse; some pinnate or more regular	Few to numerous. Central, or throughout medulla. Absent in some sections	-	-	+
<i>G. crinale</i> var. <i>luxurians</i> AHF 67180	6	200 × 100, similar throughout		As above	?	+	-	-
<i>G. crinale</i> var. <i>luxurians</i> Hollenberg 2592	1.5	150 × 190	190 × 230	As above	Scattered, but more central, in medulla	+	-	-
<i>G. crinale</i> var. <i>luxurians</i> UC 262565 (M. S. Snyder collection from La Jolla, no date)	2	250 × 150	190 × 110	Irregular, sparse	Few, in central line	+	-	-
<i>G. crinale</i> var. <i>luxurians</i> Gardner, 1927, description of taxon	to 6.5	150-200; oval to cylindrical terminally		Distichous; See pl. 46, 47	In center of fronds	-	-	+
<i>G. crinale</i> var. <i>luxurians</i> Dawson, in 1953 treatment of the taxon	to 7	150-200 in diameter, compressed to flattened		Irregular to pinnate	Few along central medullary line	-	-	+

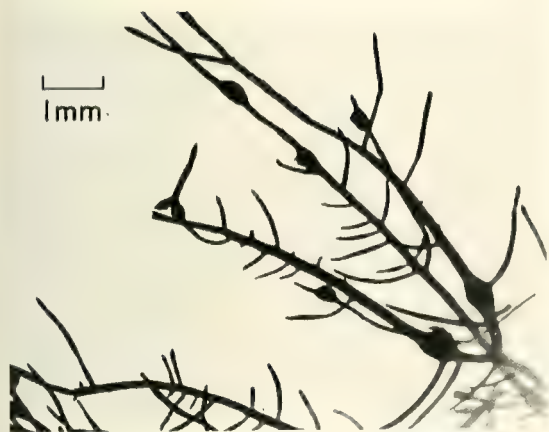


Figure 1. Unilocular cystocarps on "*Gelidium crinale* var. *luxurians*" UC 262565.

var. *luxurians*. Indeed, Gardner noted (p. 227, 1927), "This form of *Gelidium crinale* seems closely related to *G. sinicola* of this paper." The similarity between vegetative specimens of *Pterocladia media* and *Gelidium sinicola* (Table 1) makes it highly probable that the two ought to be considered synonymous although final attribution must await the finding of sexual structures in plants resembling *G. sinicola* from central or northern California.

Table 1 summarizes currently available information on the four entities outlined above. The only cystocarps observed were unilocular and occurred on plants previously identified as *G. crinale* var. *luxurians*. This taxon therefore must be transferred to the genus *Pterocladia* and the species with which the material can most appropriately be placed is *P. media*. Other collections as discussed above of undetermined *Pterocladia* are now attributed to *P. media*.

Pterocladia media Dawson

Pterocladia media Dawson 1958: 68, pl. 21, fig. 3-4, pl. 24, fig. 11; *Gelidium crinale* forma *luxurians* Collins, in Collins, Holden, and Setchell, PBA 1138 (1903); Collins 1906: 111; Gardner 1927: 277, pl. 46, fig. 1, pl. 47, fig. 3 (as var. *luxurians*).

Redescription: Thalli 3-5 (7) cm high, axes growing in tufts, simple or branched, erect portions arising from a system of stoloniferous creeping parts attached by short peg-like haptera. Branching (when occurring) irregular and sparse, generally distichous, often secund or more regularly alternate or pinnate terminally. Lateral branchlets with or without slight constrictions at point of junction with proximal axis; all axes and branches slender, narrow, mostly

of uniform dimensions from base to apices, broad, 100-200 μ m thick. Rhizoidal filaments to numerous, more often in inner medulla. Medulla relatively abundant seen throughout medulla. Cortex of several rows of pigmented cells, with all cells of similar size or with cells of inner rows as much as twice as large as cells in the outer layer. Medullary cells irregularly shaped cells, fewer than cortical cells. Tetrasporangia arranged in V-shaped rows apically on branches in some plants, in other sori without arrangement. Cystocarps develop and protrude on one surface of the apical region of a branch, typically with a single ostiole.

Infrequent or rare, in sandy patches on rock substrates, intertidal. Thalli are soft and lax, rather than stiff or cartilaginous, and slender and irregularly branched compared with *Gelidium pusillum* (Stackh.) Le Jolis which can be similar in height and habitat. Generally the latter is found in thicker clumps or dense mats. *Pterocladia capillacea* is more strikingly distichous and pinnate than *P. media* with precurrent main axes of larger dimensions than the ultimate branchlets and usually all parts are broader thus appearing more flattened than *P. media*.

In conclusion, certain algae, non-fertile but *Pterocladia*-like in vegetative characters, can now be considered as *P. media*. Southern California collections of other *Pterocladia*-*Gelidium* species are sometimes difficult to separate if cystocarps are absent. When *Pterocladia*-type cystocarps were found on some plants quite similar to Dawson's *P. media* collection (but identified as *Gelidium crinale* var. *luxurians*), Dawson's use of "*Pterocladia*" for his entity was supported, and his description could then be expanded to include both formerly undetermined plants and plants incorrectly attributed to the genus *Gelidium*. *Pterocladia media* and *P. capillacea* occur intertidally in southern California in similar habitats but can generally be recognized one from the other by the degree of branching regularity and axis breadth.

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RELATIVE STEM WATER POTENTIALS OF THREE WOODY PERENNIALS IN A SOUTHERN OAK WOODLAND COMMUNITY

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ABSTRACT: Dawn stem water potentials of *Quercus agrifolia*, *Juglans californica*, and *Heteromeles arbutifolia* were measured with a pressure chamber during the drought of 1972. Individuals of a particular species growing at the top of a slope had lower water potentials than those at the canyon bottom. These differences became greater as the season progressed and soil drying occurred. During the summer months when evaporative demands were high, leaf water deficits were not overcome during the overnight equilibration period as soil-plant water potential gradients existed in the dawn hours. *Juglans* and *Heteromeles* on the south-facing slope were able to maintain higher diurnal stem water potential maxima than corresponding individuals on the north-facing slope. This apparent anomaly may result from the more xeric conditions on the south-facing slope inducing acclimation or providing selection pressure for drought resistance of these two species.

Plant distributions depend on availability of water as much as any single environmental factor. The free energy of water in the soil and of that within plant cells is expressed by water potential (Slayter, 1967). Plant water potentials can be adequately estimated by measuring stem water potentials (SWP) in a pressure chamber (Scholander *et al.*, 1965; Waring and Cleary, 1967). This instrument has been used in a variety of studies requiring data concerning plant water potentials (Hass and Dodd, 1972; Sucoff, 1972).

It was my purpose in this study to compare the SWP of *Quercus agrifolia* Nee., *Heteromeles arbutifolia* M. Roem. and *Juglans californica* Wats. (Munz and Keck, 1959) growing at different slope positions and aspects in a Southern California Oak Woodland. This data could then be

used to explain plant densities and distributions. Since the plant density on the north-facing slope was about six times greater than that on the south-facing slope, it was expected that individuals growing at the top of the more xeric south-facing slope would have the lowest SWP.

In the only other seasonal SWP study in an Oak Woodland, Griffin (1973), working in Central California, found that bottomland *Quercus douglasii* Hook. and Arn., *Q. lobata* Nee. and *Q. agrifolia* had higher water potentials than individuals growing in upland savannas. All three

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TABLE 1. Daily percent relative humidity minima and temperature maxima on dates following the 12 August 1972 rainstorm in the Puente Hills study area.

Date	Minimum % RH	Maximum Temp. °C	Precip. mm
12	74	32.2	8.64
13	60	26.7	—
14	42	26.7	—
15	35	27.8	—

Monthly mean minimum %RH = 36.4

species had higher water potentials following a wet season than after a dry season. The deciduous *Q. douglasii* on a north-facing slope had lower water potentials than those growing on the south-facing slopes. Maximum diurnal water potentials of the evergreen *Q. agrifolia* were as low as -27 bars in August of a dry year. Since this study was also conducted during a drought year, it was hoped that the *Q. agrifolia* data would be comparable to Griffin's and that additional insight to plant distributions could be gained from looking at the other two species.

METHODS

The study area was an east-west canyon on the Weaver Ranch in the Puente Hills of southeastern Los Angeles County, California. The vegetation on the opposing north-south-facing slopes was dominated by *Q. agrifolia*, *J. californica*, and *H. arbutifolia*. The understory was primarily composed of *Sambucus mexicana* Presl., *Rhus integrifolia* (Nutt) Benth. and Hook., *R. ovata* Wats., and *R. diversiloba* T. and G. (Munz and Keck, 1959). The canyon walls were approximately equal in height (100 m) and slope (50 percent) (Rowlands, 1972). I set up four sampling stations; one at the top and bottom of each of the two opposing slopes.

At each sampling station, two to five healthy twigs were excised with a sharp razor blade from two comparable individuals each of *Quercus*,

TABLE 3. Temperature data and precipitation for the Puente Hills study area during the 1972

Month	Temperature °C		Precipitation			T
	Mean max.	Mean min.	Mean	Max.	Min.	
June	28.0	13.6	21.0	33.8	8.7	0.51
July	32.5	15.7	24.3	40.5	12.7	—
Aug.	31.5	16.5	24.2	40.5	12.2	8.64
Sept.	28.3	14.6	21.3	32.2	10.0	6.58

Juglans, and *Heteromeles*. *Quercus* sampling methods resemble those of Griffin (1973): twigs 8–15 cm long with at least three leaves. *Heteromeles* twigs were 10–15 cm long with 6–15 leaves; *Juglans* leaves were 15–25 cm long with 7–17 leaflets. All samples were collected in the pre-dawn or first light hours when the relative humidity was near its diurnal maximum and transpiration rates minimum. Samples from each species were collected normally twice a month from April through August, 1972.

Preliminary tests which contrasted on-site measurements of SWP and those of stems transported to the laboratory in humidified polyethylene bags and measured 90 minutes later, indicated no significant differences. All samples were subsequently taken to the lab where measurements were made within 60 minutes after twig excision. Sample materials were sealed into the pressure chamber and subjected to pressure increase rates of 0.5 bar sec⁻¹ as described by Waring and Cleary (1967) and Ritchie and Hinckley (1971). The balancing pressure was read at the first appearance of fluid on the reference surface of the twig or petiole.

Relative humidity was recorded daily on a hygrothermograph located 10 km northeast of the site at California Polytechnical University, Pomona (Table 1). Relative humidity was also measured on sampling days at each station with a sling psychrometer. All other climatological data (Tables 2–3) were from the U.S. Dept. of Commerce (1971–72); temperatures were from the Cal Poly Pomona Weather Station and the precipitation information was from the Walnut Patrol Station Weather Station approximately 4 km north of the site. Both weather stations are located

TABLE 2. Total monthly precipitation in the Puente Hills study area from December, 1971 to August, 1972.

Monthly Precip. (mm) Totals		
Dec 71	Feb 72	Apr 72
153.9	1.46	1.32
May 72	June 72	Aug 72
5.1	0.51	8.64

RESULTS

The data show that the individuals growing at the higher slope positions had significantly

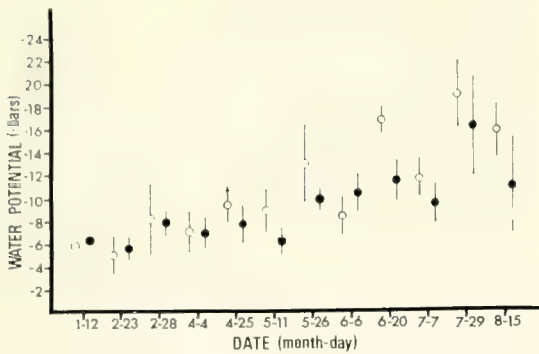


Figure 1. Stem water potentials (SWP) in -bars of *Quercus agrifolia* growing on the north-facing slope. Open circles represent mean SWP of plants at the top of the slope and closed circles those at the canyon bottom; vertical lines represent standard deviations.

($P < .05$) lower SWP than those growing at the bottom slope positions (Figs. 1–6). These relationships were not as apparent from January in the same drainage system as the study site but approximately 70 m lower in elevation.

Differences in mean SWP (Figs. 1–6) were statistically analyzed using a randomized complete-block design (Steel and Torrie, 1960) analysis of variance in which the sampling dates were used as blocks.

through April as they were during the summer months. Higher relative humidities and lower temperatures were observed throughout the study at the lower sampling stations. The few instances in which this slope-position difference was reversed were probably the result of sampling error.

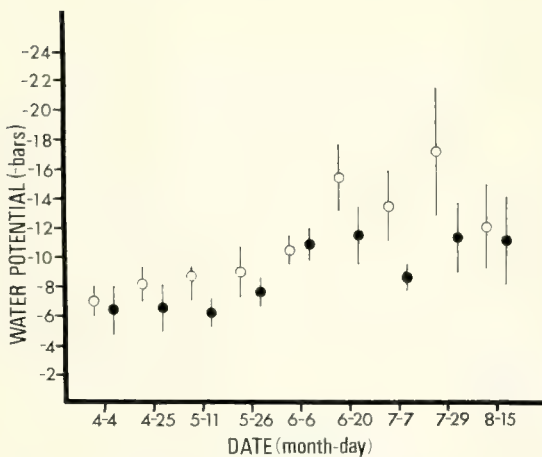


Figure 2. SWP of *Quercus agrifolia* growing on the south-facing slope. (See Fig. 1)

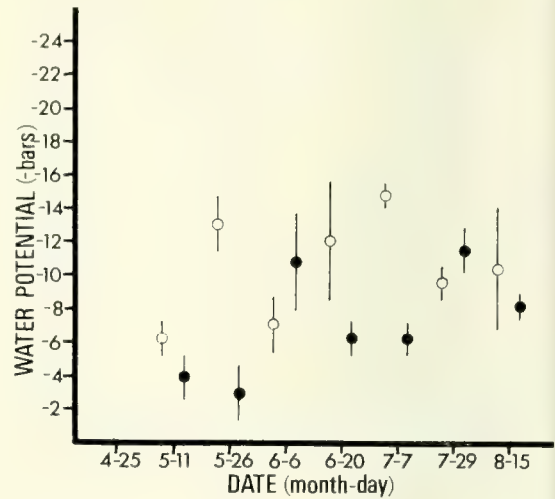


Figure 3. SWP of *Juglans californica* growing on the north-facing slope. (See Fig. 1)

All SWP showed a significant ($P < .05$) decrease from spring to summer (Figs. 1–6). July was the warmest, driest month of the summer as temperatures ranged from 12.7–40.5°C and there was no precipitation (Table 3). Although the area received 8.64 mm of precipitation the morning of 12 August, it probably had no effect on soil moisture in the root zone as the temperature reached 32°C that afternoon and was followed by subsequent days of high temperatures (Table 1). All SWP increased between 29 July and 15 August. There is a difference ($P < .07$) between the SWP from the north and south-facing slopes.

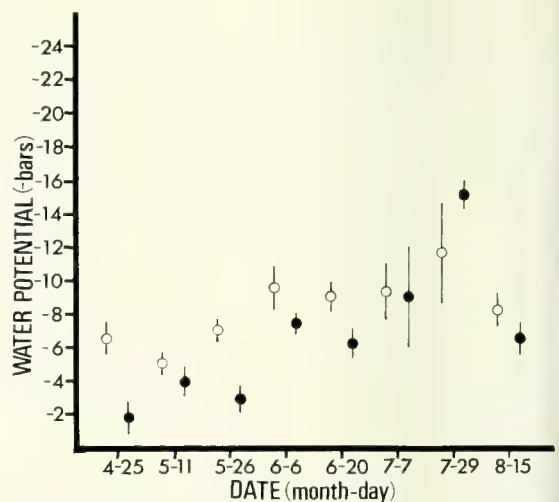


Figure 4. SWP of *Juglans californica* growing on the south-facing slope. (See Fig. 1)

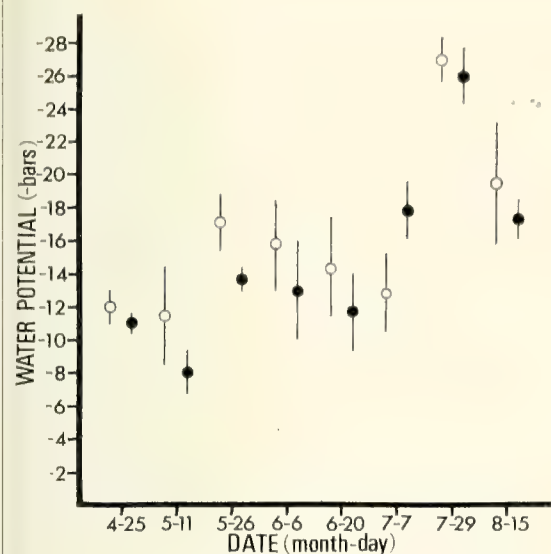


Figure 5. SWP of *Heteromeles arbutifolia* growing on the north-facing slope. (See Fig. 1)

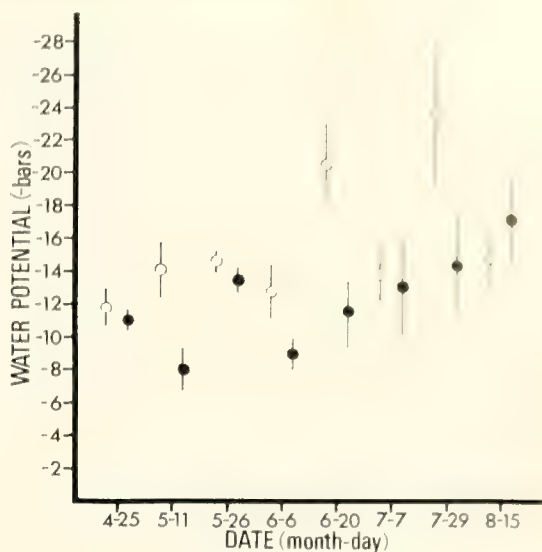


Figure 6. SWP of *Heteromeles arbutifolia* growing on the south-facing slope. (See Fig. 1)

On most sampling days, *Juglans* and *Heteromeles* growing on the more xeric south-facing slope had higher SWP than that of the same species on the north-facing slope (Figs. 3–6). The lower SWP of *Juglans* on the north-facing slope are more dramatic and are lower there than on the south-facing earlier in the spring (Figs. 3–4).

Interspecific differences make SWP comparisons difficult unless these differences are accounted for (Boyer, 1967; Kaufmann, 1968). Ritchie and Hinckley (1971) reported that the magnitude of the error between stem and leaf water potentials and between SWP of different species is minimum at high water potentials. Since all data are near the diurnal maxima, comparisons can be made (cautiously) on a relative basis even though measurements were made on *Quercus* and *Heteromeles* twigs and on *Juglans* leaves. These comparisons can be helpful in understanding distributional differences.

There is a significant ($P < .05$) difference in the SWP of the three species. *Heteromeles* generally had the lowest SWP followed by *Quercus* and *Juglans* which generally had the highest values (Figs. 1–6). Distributionally, *Quercus* was most important (referring to importance value indices, Shimwell, 1971) on the north-facing slope and canyon bottom (presumably the more mesic sites); *Juglans* was most important on the south-facing slope on which *Heteromeles* was relatively rare (Rowlands, 1972).

DISCUSSION

When soil water is not limiting, dawn soil and plant water potentials can be assumed to be equal even though leaf water deficits occur daily. When soil water becomes limiting or when high evaporative demands cause extreme leaf water deficits, however, the overnight equilibration period may not be adequate to overcome internal plant water deficits (Slayter, 1967). In this case, dawn plant water potentials would be lower than soil water potentials. Soil water potentials were probably higher at the canyon bottom due to down-slope water movement both as surface run-off and subterranean percolation. This would also result in a shallower water table at the canyon bottom. These facts along with lesser evaporative demands brought about by lower temperatures and higher relative humidities at the canyon bottom, explain the slope-position differences observed in all species. Since soil drying would occur faster on the slopes than at the base of the canyon, the general water potential decrease and the slope-position differences became more apparent as the dry season progressed. December rains may have wet soil profiles but precipitation in subsequent months was far below normal (Table 2). The rainstorm on 12 August which increased relative humidity minima on subsequent days (Table 1), decreased evaporative demands (and consequent leaf water deficits) and allowed all species to show an increased SWP between the 29 July and 15

August samples (Figs. 1–6) by enabling the soil and plant water potentials to approach equilibria. If one ignores the 29 July data, because the dawn values may reflect a soil-plant water potential gradient due to the previous days extreme leaf water deficits, the curves approximate more closely typical drying trends.

The generally higher SWP observed for south-facing slope *Juglans* and *Heteromeles* relative to the values recorded on the north-facing slope are opposite from what one would expect. Individuals growing on the more xeric south-facing slope should exhibit lower SWP than those on the more mesic north-facing slope. Soil water should be less and leaf water deficits greater on the south-facing slope due to greater evaporative demands. There must be some mechanism that enables these plants to respond in this manner.

Shropshire (1972) compared physiological responses of *H. arbutifolia* that were grown in a mesic-conditioned environmental chamber with those grown in a garden under more xeric conditions. When both groups were subjected to relatively dry air, the plants grown under mesic conditions closed their stomates within 1.5 hours (stopping transpiration and CO_2 exchange); the garden grown plants were able to maintain reduced gas exchange for 3.5 hours. She felt that the stomates of this species were in some way capable of acclimating to xeric environmental conditions which enabled them to continue gas exchange in dry air. Plants that had been acclimated to drier conditions were better able to maintain lower leaf water deficits or overcome these deficits than plants that were acclimated to mesic conditions. Lower water deficits should be reflected in the dawn SWP of plants grown in different habitats and can be used to explain my results.

Since the 1971–72 season was one of the driest on record for Southern California (U.S. Dept. of Commerce, 1972), soil on both slopes probably had unusually low water potentials. Because the south-facing slope is characteristically more xeric, individuals on that slope would be acclimated to drier conditions than those on the opposing slope. This acclimation could be accomplished by any morphological or physiological modification (be it genetic or phenotypic) that would result in a reduction of water usage. This environmental pre-conditioning would have enabled the south-facing slope *Heteromeles* and *Juglans* to recover more quickly from daily leaf water deficits that occurred during the extreme drought. *Heteromeles* demonstrates a smaller north-south disparity than

Juglans (Figs. 3–6). Although *Heteromeles* has deep tap roots (Hellmers *et al.*, 1955), it probably is not rooted into the water table as is *Juglans* (T. L. Hanes, pers. comm.). The less extensive root systems of shrubs may negate any acclimation advantage since upper profiles were dry on both slopes. This also explains why *Heteromeles* had generally lower SWP than the two species of trees. It is possible that *Juglans* is more responsive to previous environmental selection.

Griffin (1973) reported that *Q. douglasii* growing on the north-facing slopes had lower SWP than those on south-facing slopes. He attributed this disparity to increased root densities on the north-facing slopes which depleted soil water. The north-facing slope which I studied also was much more densely vegetated having approximately six times the density of the south-facing slope. *Quercus* shows no consistent north-south relationship; soil water potential data would be helpful in interpreting these SWP values. Greater root densities should be found where there is more soil water and hence higher SWP values.

It is possible that SWP measurements were made when the plants were transpiring due to an immediate response to the first light of dawn. Since the plants at the top of the slope are exposed to dawn light before the individuals at the canyon bottom, their stomates might open earlier and subsequent leaf water deficits would establish a water potential gradient earlier in the morning. Northeast-facing slope plants receive the earlier summer dawn light and hence establish water potential gradients sooner than do south-facing slope individuals. Interspecific water potential differences could be explained simply by differential metabolic water requirements. Further research needs to be done to determine the relative sequence and amount of light on a particular slope necessary to cause stomatal response in these species.

Interspecific comparisons of transpiration rates, diurnal water potential curves and leaf water deficit recovery time should be made. It is possible that there is more water available to the south-facing slope plants due to substrate, root depth, and density differences and it would be interesting to re-examine this area in a normal rainfall season to see if these species would respond in the generally expected north-south slope manner. Seasonal soil water potential and water table information would be instructive in the further understanding of soil-plant relationships in these woody perennials.

ACKNOWLEDGMENTS

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RESEARCH NOTES

THE FIRST REPORT OF THE GIANT POLYNOID POLYCHAETE *HOLOLEPIDA* *MAGNA* MOORE FROM CALIFORNIA

Moore (1905) described a new genus and new species of a giant polynoid scaleworm, *Hololepida magna*, from a single specimen measuring 25 cm and possessing 120 segments. It was collected by the Albatross expeditions from Kasaan Bay, Prince of Wales Island, Alaska (corrected locality, Moore, 1908) from 173.7–198.5 m. Later Berkeley (1923) reported two specimens, length not specified, from 27.4–36.6 m depth near Nanaimo, British Columbia. This species has not been reported since that date.

Recently specimens of what proved to be *H. magna* were turned over to me for identification by personnel from both the Los Angeles City and County Sanitation Districts. These specimens were collected by trawling in connection with monitoring programs. In discussion of this species with the late Olga Hartman, she showed me a specimen, previously unreported, dredged from Monterey Bay, California on 12 February 1931 by G. E. MacGinitie. The data on these new reports are summarized below. The lengths and number of segments given represent minimal figures since this species readily fragments.

Monterey Bay, 1 specimen, length 11.6 cm, 83 segments; collected by G. E. MacGinitie, 12 February 1931.

Santa Monica Bay, 2 specimens, length 22.9 and 21.6 cm, 94 and 96 segments, depth 54–8 m, collected by Los Angeles City Sanitation District on 31 May 1972.

Palos Verdes Peninsula, 5 specimens, 1 measured 20.3 cm, 4 specimens fragmented, 89 segments, depths 59–137 m, collected by Los Angeles Sanitation District on 2 June 1972 (3), 14 June 1973 (1), and 5 December 1973 (1).

Superficially this genus resembles a sigalionid more than a polynoid because of its large size, the large number of elytrae and the occurrence of elytrae on every posterior segment, but it can be readily distinguished from a sigalionid by the presence of dorsal cirri on segments lacking elytra. The possession of the nuchal hood (Fig. 1) distinguishes this genus from the other polynoid genera. Three species of the genus *Hololepida* are brown and may be separated as follows:

H. magna: Prostomium deeply incised anteriorly; nuchal hood triangular; neuropodial bidentate

setae strongly serrated with the two teeth of nearly equal length (Moore, 1905:541). Eastern Pacific Ocean.

H. australis: Prostomium weakly incised anteriorly; nuchal hood rectangular; neuropodial bidentate setae strongly serrated (Monro, 1936:93). Falkland Islands.

H. veleronis: Prostomium deeply incised anteriorly and with lateral lobes produced and rounded anteriorly; nuchal hood triangular; neuropodial bidentate setae weakly serrated (Hartman, 1939:48). Gulf of California.

All specimens of this genus were obtained by dredging and all were fragmented during the process of collection. Undoubtedly more specimens of *H. magna* will be encountered in the future especially as a result of the initiation of additional monitoring programs. The fact that the southern California specimens were collected in connection with monitoring domestic sewage discharges does not necessarily imply that this species is an indicator of polluted conditions.

The author wishes to acknowledge thanks to Jan Stull, Los Angeles County Sanitation District and to Leland Hill, Los Angeles City Sanitation District for referring the material to me.

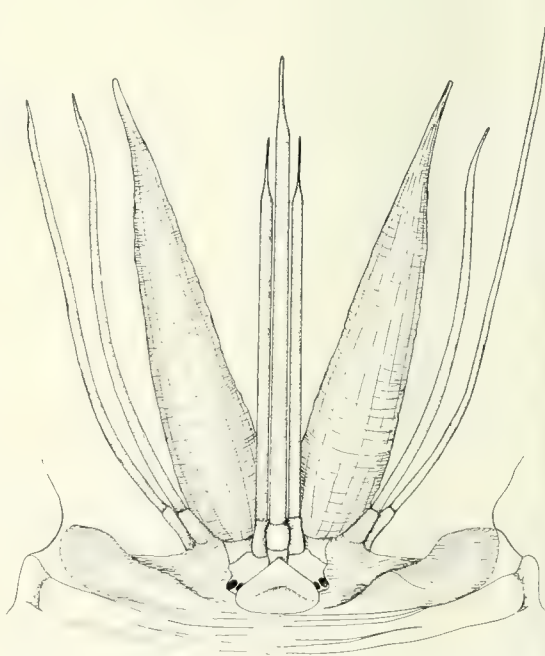


Figure 1. *Hololepida magna*, anterior end, dorsal view.

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NUTRITIVE VALUE OF
THREE COMMON CHAPARRAL
PLANTS FOR THE WOODRATS,
NEOTOMA FUSCIPES AND *N. LEPIDA*

The food values of different plants to woodrats have commonly been inferred from stomach contents, feces composition and nest caches (Horton and Wright, Ecology, 25:341-351, 1944; Linsdale and Tevis, The dusky-footed woodrat, 1951; Cameron, J. Mamm., 52:288-296, 1971). The actual nutritive value of a plant can only be determined by following a physiological index, such as body weight, during feeding trials. Only if there is a positive result can one say that a particular item is a physiologically available food (Chess and Chew, J. Mamm., 52:193-195, 1971).

Three common chaparral plants were fed to *Neotoma fuscipes* (Dusky-footed woodrat), a characteristic chaparral rodent, and to *N. lepida* (Desert woodrat), typical of desert areas, but found in a great variety of vegetation types (Cameron, 1971). The *N. fuscipes* we used were trapped in the Santa Monica Mts. and San Gabriel Mts. in typical chaparral. The *N. lepida* were from near Mitchell Caverns, San Bernardino Co, California, from a desert community dominated by *Larrea tridentata*, *Opuntia* spp.,

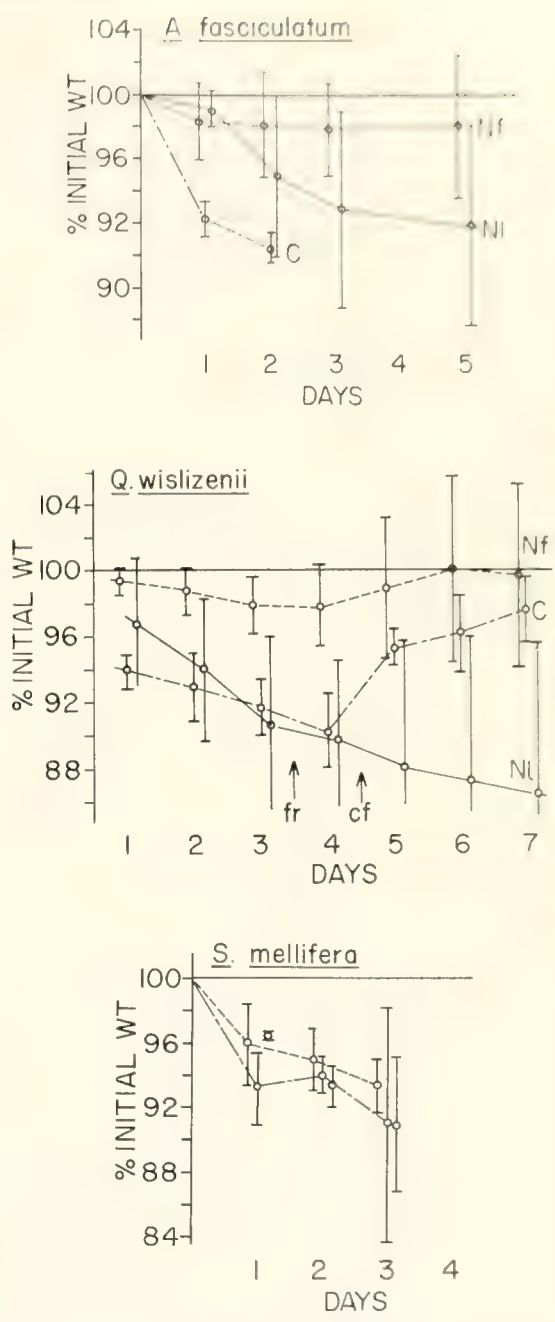


Figure 1. Body weight changes of woodrats fed on diets of a half maintenance ration of Purina Laboratory Chow and a surplus of the leaved stems of: (a) *Adenostoma fasciculatum*, (b) *Quercus wislizenii*, and (c) *Salvia mellifera*. Dashed line connects means for *Neotoma fuscipes*; solid line, *N. lepida*; broken line, control group of *N. fuscipes*, fed only half ration of chow. Vertical lines are the range of mean $\pm$ 2 standard errors. In figure 1c the average values for *N. lepida* are not connected, in order to reduce confusion of lines.

and *Yucca schidigera*. The plant species used were *Adenostoma fasciculatum* (chamise, an evergreen shrub), *Quercus wislizenii* (evergreen oak, a tree), and *Salvia mellifera* (black sage, a deciduous shrub). Chamise and one species or another of evergreen oak are common dominants in chaparral of southern California, and consequently they are potentially important food plants for woodrats. Linsdale and Tevis (1951) rated chamise and live oaks as Class 1 foods, most eaten food plants of *N. fuscipes*, on subjective grounds. *Salvia mellifera* is dominant only in the coastal sage type of chaparral; we chose it because it has a strong odor from volatile oils, which might be deterrents to feeding. Linsdale and Tevis rated black sage as a Class 4 food, least eaten; black sage and several other odoriferous species were characterized as "not a well liked food" by *N. fuscipes*.

The woodrats were kept at room temperature in $25 \times 30 \times 60$ cm wire mesh cages with woodchips and shredded newspaper bedding and water as desired from a drinking bottle. During a preliminary period we determined the minimum amount of Purina Laboratory Chow that was necessary for each animal to maintain body weight. Weights averaged 182 g (108–238 g) for *N. fuscipes* and 102 g (79–143 g) for *N. lepida*. During a feeding trial each animal was given one half of its maintenance ration of chow plus an excess of leaved stems of one of the plants. Plants were freshly collected at the beginning of each trial (unless noted otherwise) and kept with their stems in water. A control group of three *N. fuscipes* was given only the half chow ration. Rats were weighed daily at the same time; weights were expressed as a percentage of the initial weight. The woodrats ate leaves and bark of *Q. wislizenii*, but only leaves of the other two species. They used stems of all species to make "nests" in their cages.

Body weight changes on the different diets are shown in figure 1. If the ranges of ± 2 standard errors do not overlap, or overlap only slightly, one can assume statistical significance ($P \leq 0.05$). The standard errors are usually large due to small sample sizes (3–5 animals) and wide individual variation. The loss of weight of the controls is a baseline for interpretation of the nutritive value of the plant part of the diet.

As shown in figure 1a and 1b, *A. fasciculatum* and *Q. wislizenii* were sufficiently nutritious to allow *N. fuscipes* to maintain normal weight (i.e. a weight not significantly different from initial weight). All *N. lepida* lost weight on these plants; their average weights were not significantly different

from the controls, which were starving on a half ration of chow. The nutritive value of the oak seemed to be affected by its freshness. The first feedings were with stems picked 10 days before the first feeding. Although the stems were kept in water, the *N. fuscipes* fed on them dropped significantly below initial weight, although they were significantly above the controls. When fresh stems were given to both experimental groups beginning in the fourth day (fr in Fig. 1b) the weights of *N. fuscipes* returned to normal. *Neotoma lepida* continued to lose weight, but at a slower rate. When the control group was given fresh oak stems beginning in the sixth day (cf in Fig. 1b), they recovered their lost weight. The lesser value of the "old" oak stems causes us to wonder about the food value of stems found in woodrat nests. The continual loss of weight of *N. lepida* on the oak was surprising in view of Cameron's (1971) report that *N. lepida* in Joshua Tree National Monument had a diet mainly of *Quercus turbinella*, another evergreen species. But, *Q. wislizenii* is a plant that is foreign to the experience of the population of *N. lepida* that we sampled. The maintenance of weight of our *N. fuscipes* on chamise is not consistent with the unsupported statement of Linsdale and Tevis (1951:278) that "chamise foliage . . . will not sustain the rats."

Neither species of woodrat was able to maintain weight on *S. mellifera*, and they washed themselves excessively after beginning to eat the leaves. One *N. fuscipes* was unable to regain normal weight after the trial, even when given additional succulent foods (carrots and celery). The volatile substances may have had some effect on the functioning of the digestive tracts of the rats, as do oils of sagebrush for deer (Nagy *et al.*, J. Wildlife Mgmt., 28:785–790, 1964).

Learned or inherited behavior may be involved in the inability of our *N. lepida* to maintain weight on any of the three plants, which are all foreign to their environment. Lee (Univ. California Publ. Zool., 64:57–96, 1963) found differences in the way experienced and naive woodrats fed on *Opuntia*. Without further tests we are unwilling to conclude that there is a real difference in the nutritive value of chamise and oak for the two species of *Neotoma*.

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INSTRUCTIONS FOR AUTHORS

The BULLETIN is published three times each year (April, August, and November) and includes articles in English in any field of science. Non-members will be assessed a page charge of \$40.00 per page. Manuscripts submitted for publication should contain results of original research, embrace sound principles of scientific investigation, and present data in a clear and concise manner. The current *AIBS Style Manual for Biological Journals* is recommended as a guide for contributors. Consult also recent issues of the BULLETIN. Authors should strive for directness and lucidity, achieved by use of the active voice. Special attention should be given to consistency in tense, unambiguous reference of pronouns, and logically placed modifiers.

MANUSCRIPT PREPARATION

It is strongly recommended that, before submitting a paper, the author ask qualified persons to review it. The author is requested to submit *at least one additional copy with the original*, on 8½ × 11 opaque, non-erasable paper, double spacing the entire manuscript. *Do not break words at right-hand margin anywhere in the manuscript.* Footnotes should be avoided. Manuscripts which do not conform to the style of the BULLETIN will be returned to the author.

An abstract summarizing in concise terms the methods, findings, and implications discussed in the paper must accompany a feature article.

A feature article comprises approximately five to thirty typewritten pages. Papers should usually be divided into the following sections: abstract, introduction, method, results, discussion, conclusions, and literature cited. Avoid using more than two levels of subheadings.

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Abbreviations: Use of abbreviations and symbols can be determined by inspection of a recent issue of the BULLETIN. Omit periods after standard abbreviations: 1.2 mm, 2 mi, 30 cm, but Figs. 1-2. Use numerals before units of measurements: 5 ml, but nine spines (10 or numbers above, such as 13 spines). The metric system of weights and measurements should be used wherever possible.

Taxonomic procedures: Authors are advised to adhere to the taxonomic procedures as outlined in the International Code of Botanical Nomenclature (Lawjouw *et al.*, 1956), the International Code of Nomenclature of Bacteria and Viruses (Buchanan *et al.*, 1958), and the International Code of Zoological Nomenclature (Stoll *et al.*, 1961). Special attention should be given to the description of new taxa, designation of holotype, etc.

The literature cited section should include six or more references; entries for books and articles should take these forms.

McWilliams, K. L. 1970. Insect mimicry. Academic Press, vii + 326 pp.

Holmes, T. Jr., and S. Speak. 1971. Reproductive biology of *Myotis lucifugus*. J. Mamm., 54: 452-458.

Brattstrom, B. H. 1969. The Condor in California. Pp. 369-382 in Vertebrates of California. (S. E. Payne, ed.), Univ. California Press, xii + 635 pp.

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(McWilliams, Insect mimicry, p. 216, 1970); (Holmes and Speak, J. Mamm., 54: 452-458, 1971); (Brattstrom, The Condor in California, Pp. 369-382, in Vertebrates of California, 1969).

Tables and figures (line drawings, graphs, or black and white photographs) should not repeat data contained in the text. The author must provide numbers and short legends for tables and figures and place reference to each of them in the text. Legends should be typed on a separate sheet of paper and placed at the end of the manuscript. Illustrations and lettering thereon should be of sufficient size and clarity to permit reduction to standard page size; ordinarily they should be no more than twice the size intended for reduction and should not exceed 8½ by 11 inches in size. Photographs must be printed on glossy paper. Submit one photoduplicated copy of each illustration. All illustrations accompanying Research Notes must be reduced to one column width.

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COVER: California gray whale, *Eschrichtius robustus*, from off Islas Coronados, Baja California, Mexico.

Photo by Stephen Leatherwood, courtesy Naval Undersea Center.

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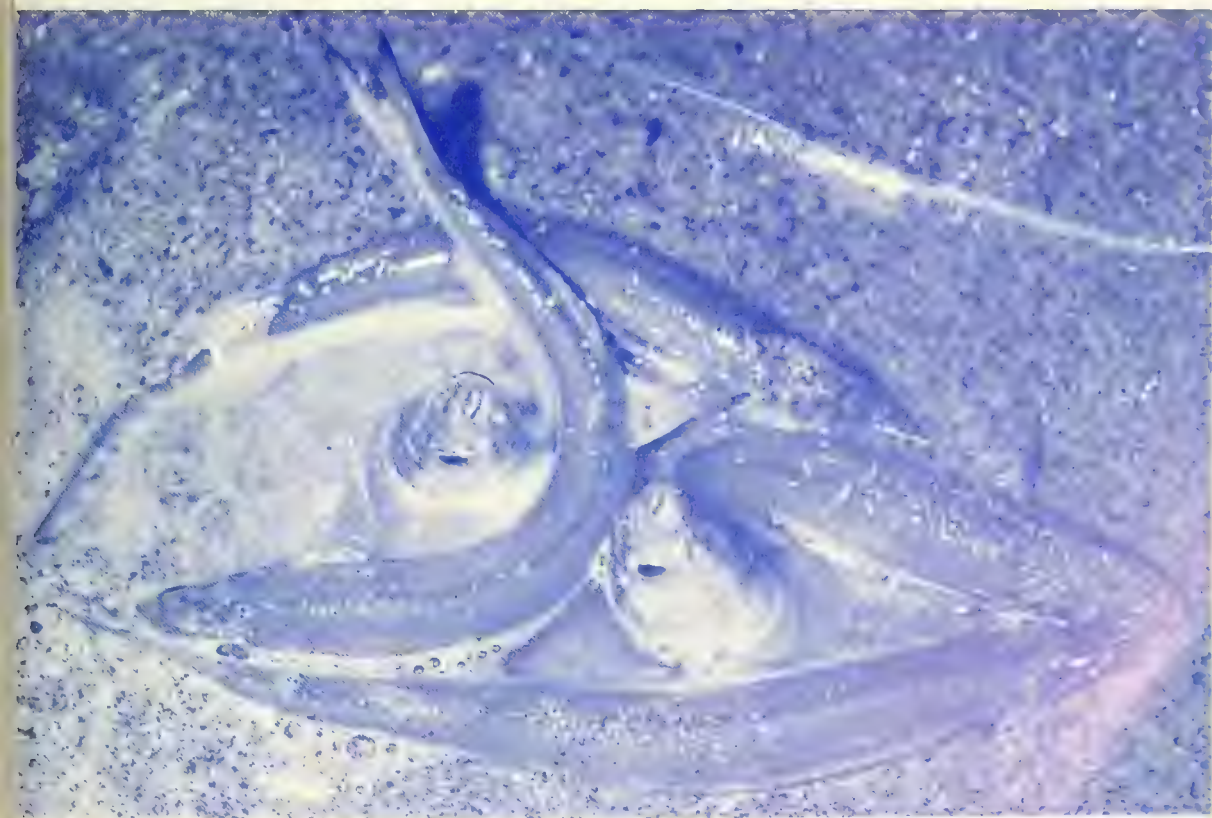
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TUBE DWELLING BEHAVIOR IN THE MARINE ANNELID
PHRAGMATOPOMA CALIFORNICA (FEWKES)
(POLYCHAETA: SABELLARIIDAE)

PETER ALAN ROY¹

ABSTRACT: Abdominal tentacles position the body centrally in the tube, permitting lateral and dorsal body cilia to draw in water ventrally, pass it up between the parapodia, and expel it dorsally. Withdrawal involves contraction, peristalsis, and backward parapodial walking. Extensions of the parathoracic palps effect forward locomotion, and parathoracic neurosetae cause body twisting. In defecation abdominal neurosetae pass fecal strings anteriorly where a body retraction expels them ventrally from the tube.

Members of the polychaete family Sabelliidae are suspension feeders that live in blind tubes of cemented sand grains and shell fragments. Anatomically and behaviorally they are adapted to a tube dwelling existence. Studies on the biology of the Sabelliidae have centered on morphology, embryology, larval behavior, and tube and reef building. The behavior of adult animals is still incompletely known. McIntosh (1922) included the observations of Arnold Watson on the natural history and anatomy of *Tetereus* (*Pallasia*) *murata* (Allen), *Sabellaria spinulosa* Leukart, and *S. alveolata* (L.). Wilson described the development and settling behavior of the larvae of *S. alveolata* (1929, 1968a, b, 1970a) and *S. spinulosa* (1929, 1970b). Wilson (1969) also described the natural history and defecation behavior of *S. alveolata*. Dales (1952) considered the development and structure of the anterior end of *Phragmatopoma californica* (Fewkes), and included observations on the ciliary tracks of the feeding tentacles and the food grooves leading to the mouth. Vovelle (1957a, b, 1958a, b, 1963, 1965) described the structure and construction of the tubes and the formation of colonies in *S. alveolata*. He noted that an adult worm removed from its tube was unable to build a new one. Kaestner (1967) briefly mentioned water currents within the tube, and noted they are responsible for irrigation and defecation. Kirtley's (1968) account of *P. lapidosa* (Kinberg) described the processes of

tube building, the ciliary and feeding currents, peristaltic pumping, locomotion, and defecation of this worm.

While these accounts contribute much valuable information, the picture of the activities of a worm within its tube is not yet complete; the objective of the present paper is to fill this gap. Studies have centered on how the animal maintains its position and posture within the tube, the manner in which withdrawal and forward locomotion occur, the circulation of water within the tube by ciliary and other means, and the mechanism of elimination of fecal matter from the tube.

METHODS

Studies were conducted at the Hopkins Marine Station of Stanford University, Pacific Grove, California. Colonies of *Phragmatopoma californica* abound on the intertidal rocks between Mussel Point and Point Alones, adjacent to the marine station. Portions of colonies taken in the field were maintained in good condition for as long as five months in tanks of running seawater (14°–16° C) in the laboratory.

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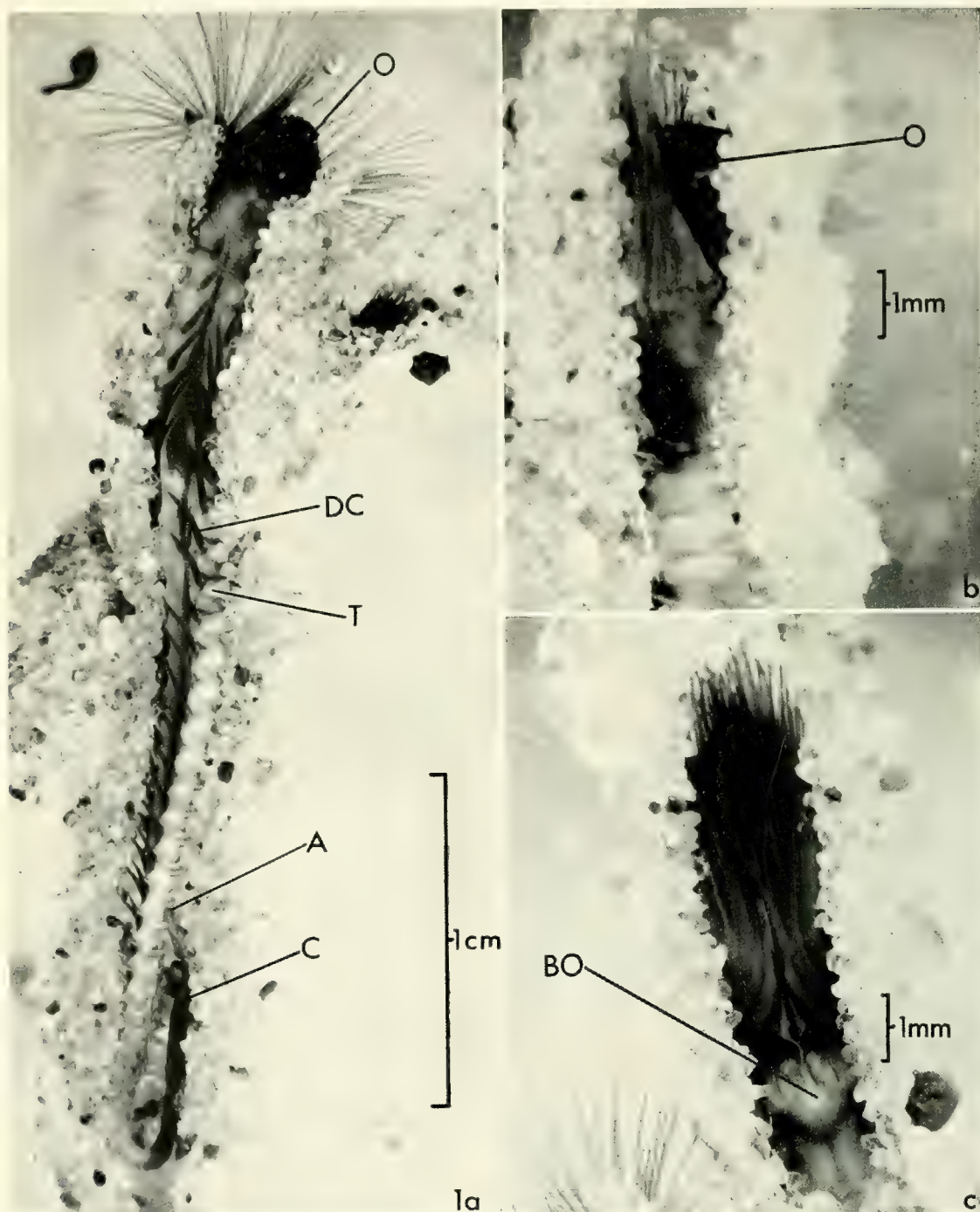


Figure 1. *Phragmatopoma californica* in sand tubes constructed against glass. a. Worm in expanded position with the body twisted; dorsal surface exposed anteriorly and ventral surface posteriorly. b. Worm withdrawn into its tube, left side of anterior region. c. Worm withdrawn into its tube, anterior region, ventral side. A, anus; BO, building organ; C, cauda; CB, ciliary band; DC, dorsal cirrus; FG, food groove; M, mouth; NS, neurosetae; O, operculum; P, palae; PX, parathorax; PT, prostomal tentacle; T, torus; VC, ventral cirrus; VP, ventral plate.

For studies of ciliary tracts on the body, specimens were first removed from their tubes and anesthetized with a solution of magnesium chloride isotonic with seawater (7.4 percent $MgCl_2$ by weight). The worms were then replaced in seawater and a suspension of colloidal graphite (Aguadag, Acheson Colloids Co.) was added. For observations of living worms in tubes, a transparent tube preparation was developed. Worms taken in the field were brought into the laboratory and distal portions of the tube broken off until the worm was left with only enough tube to contain its fully contracted body. These worms were placed in petri dishes without lids, and the dishes submerged in an aquarium. Sand was sprinkled over the dishes until a layer 1–2 grains thick was present on the bottom. The worms extended partially from their tubes, and with this sand they constructed extensions of their original tubes against the bottom of the dish. These extensions were arches of sand built against the glass with the glass forming part of the tube wall. Additional sand was added daily as needed. If too much sand was provided the extension would be a complete cylinder of sand, at least in spots, obscuring subsequent observations. Within 2–3 days worms had constructed tube extensions 1–3 times their body length. At this time the original posterior portion of the tube was broken off and sand was sprinkled over the resulting posterior hole. This was shortly cemented in place by the worms, closing the posterior end of the tube and leaving the animal in a tube of sand built against the glass, allowing clear vision of the entire body (Fig. 1a).

For observation and photography, the top of the petri dish was added, and the whole dish inverted under water. A suspension of carbon particles was added to facilitate the study of currents within the tube. Except in special instances worms were always completely immersed in water during observation, and the water was changed frequently to keep it cool. Drawings were made with a camera lucida.

RESULTS

Morphology of Phragmatopoma californica.—

The body of *P. californica* is about 2–3 cm in length and as in other sabellariids is composed of four regions: head, thorax, abdomen, and cauda (Fig. 3a, b). The head (Dales, 1952) includes the operculum, opercular stalk, feeding tentacles, mouth, and building organ. The thickened muscu-

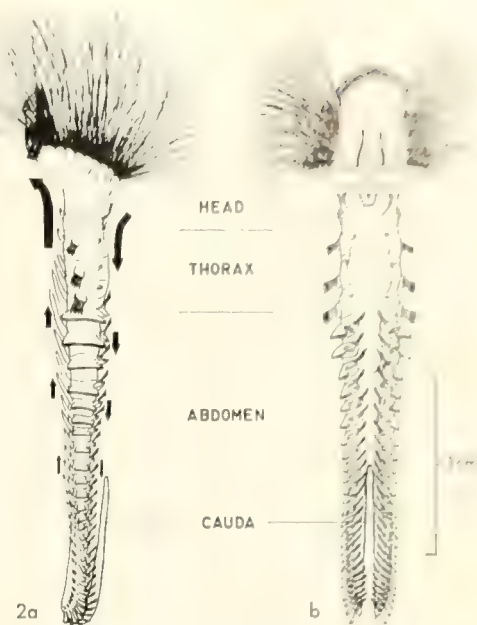


Figure 2. *Phragmatopoma californica*; entire animals, in expanded posture. Arrows show major circulation of water around the body. a. Lateral view of right side. b. Ventral view.

lar thorax consists of five segments, the posterior four of which bear large dorsal cirri. The posterior three segments of the thorax are the parathoracic segments, and these bear spear-shaped notopodial palae and capillary neurosetae. The palae are smallest in the first parathoracic segment and largest on the third segment, while the reverse is true of the neurosetae. Ventrally the parathoracic segments form a muscular ventral plate. The abdomen consists of 20–40 rather similar segments, all bearing dorsal cirri which, as those of the thorax, possess blood vessels with a pulsating blood flow. The abdominal notopodia are uncinigerous tori. Each neuropodium consists of a ventrolateral lobe bearing capillary neurosetae and lateral to it a broad fleshy lobe referred to as a "ventral cirrus" by McIntosh (1922). There is a gradual reduction in size of the dorsal cirri and tori from the first abdominal segment on back so that posteriorly the cirri are reduced to papillae and the tori to elongate, stiff, paddle-shaped projections. The abdomen is flattened ventrally, forming a groove that extends from the posterior margin of the ventral plate to the origin of the cauda. The cauda, a cylindrical terminal region of the body lacking parapodia

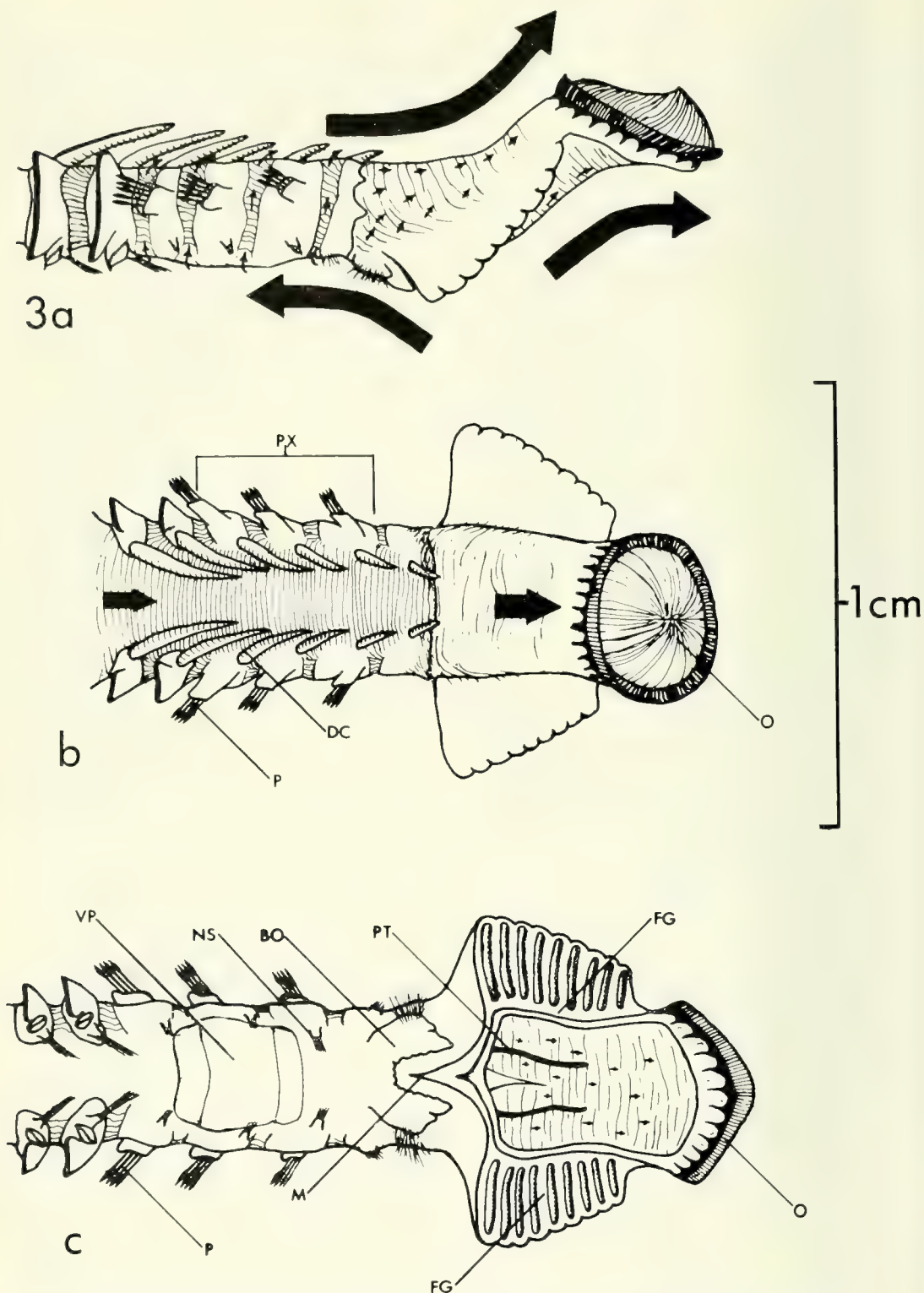


Figure 3. Anterior body regions of *Phragmatopoma californica*, with feeding tentacles removed. Small arrows show the direction of ciliary beat; large arrows indicate the major flow of water over the body. a. Lateral view from right side. b. Dorsal view. c. Ventral view. See figure 1 for key to abbreviations.

and external signs of segmentation, is reflected ventrally and anteriorly. It extends forward within the concavity of the abdomen for one-third to one-half the total length of the abdomen. The anus is at the tip of the cauda.

Building of the tube extension and posture within the tube.—Tube building by worms in glass dishes indicates that sand particles need not be in suspension to be used for construction. Any particles of sand contacting the head tentacles are passed by cilia to the mouth and then to the building organ where the grains are coated with cement. The head is then protruded and the grain manipulated into position and cemented at the mouth of the tube by the building organ. Tubes built against glass in the laboratory were thinner at their open ends and lacked the flared apertures normally present in colonies found in the field. However, tubes of solitary specimens of *P. californica*, which are built against surfaces of intertidal rocks around Hopkins Marine Station, also lack flared apertures and are otherwise similar to the tubes constructed in the laboratory.

In natural colonies the head and thorax of an expanded worm lie within the flared tube opening. The opercular stalk is bent dorsally so that the feeding tentacles radiate outward beyond the tube mouth. Expanded worms in tubes constructed against glass behaved similarly in all respects except that they protrude their opercula a little beyond the tube opening in order to fully extend the feeding tentacles (Fig. 1a).

The worm occupies a central position within the tube along the tube axis leaving room for water to circulate on all sides. The body is braced in this position laterally by extension of the abdominal tori on each side so that their uncinigerous margins contact the tube wall. Ventrolaterally, the neuropodial "cirri" are braced against the tube wall and aid in the positioning of the body especially posteriorly where the notopodial tori are long and attenuated. Although the anteromedially directed abdominal neurosetae may contact the tube wall, they are not critical in maintaining normal position of the body in the tube. The thorax is braced in a central position by the posterolaterally directed parathoracic palae. The parathoracic neurosetae, directed antero-ventrally, and the neurosetae of the first abdominal segment, hold the thorax elevated above the floor of the tube. Worms are often observed to be twisted through 90° to 180° along the axis of their bodies (Fig. 1a).

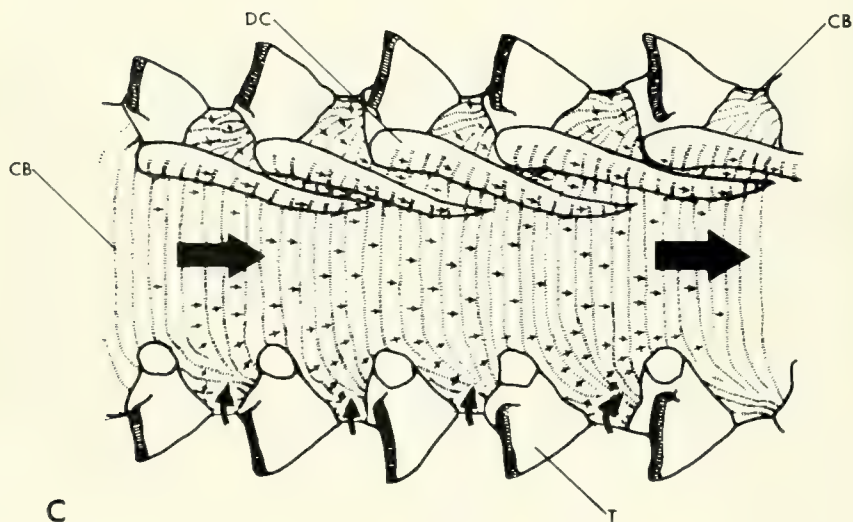
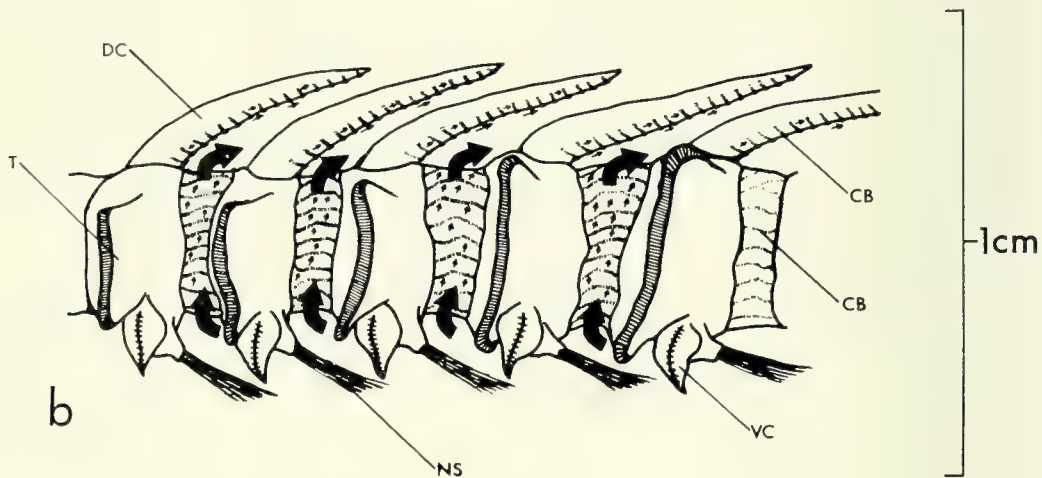
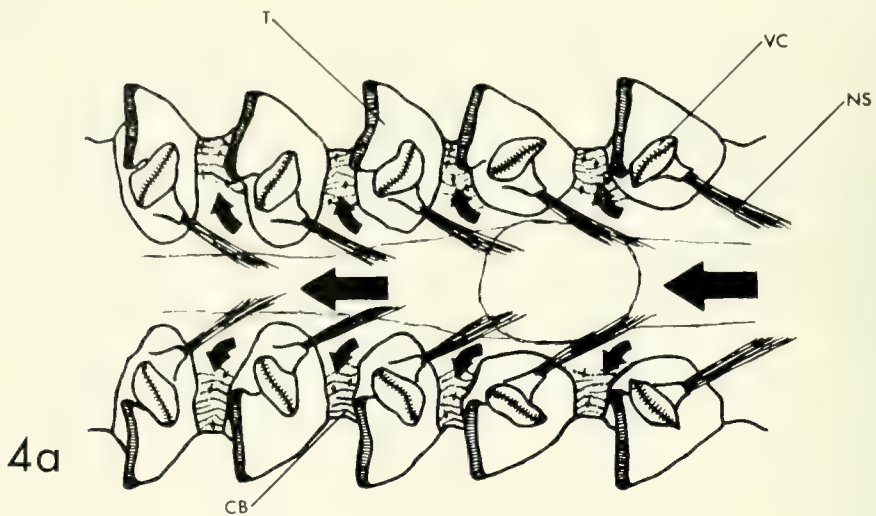
Withdrawal response and back

Like other sedentarians, *P. californica* rapidly withdraw its exposed head and tentacles into its tube. When the feeding tentacles are rapidly contacted the opercular stalk is bent ventrally to the tube (Fig. 1b, c). Simultaneously the worm withdraws the anterior two-thirds of its body so that the palae and tori of this region lose contact with the tube wall. The posterior tori and perhaps the neuropodial cirri maintain contact as an anchorage. Then the worm withdraws its anterior end into the tube by shortening the body.

If the stimulus is sufficiently strong or is continued, the animal backs further into the tube. This is accomplished in two ways. The first action is monotaxic and involves body peristalsis. The parathorax is expanded after completion of the initial withdrawal response. This increases its diameter and anchors the anterior body in the withdrawn position. Then the abdomen constricts, loses contact with the tube wall, and is elongated and extended posteriorly where the tori gain a new posterior anchorage. Finally the thorax constricts and the body shortens, withdrawing the anterior portions, completing the cycle. The second method of backward locomotion is slower than the first and involves parapodial walking. In walking backward nearly the whole body loses lateral contact with the tube wall. The posterior abdominal tori maintain an anchorage. Backward movement of the body is initiated by rear-to-front walking motion of these posterior tori. Only the projecting tori of the last 6–10 abdominal segments are involved, and the activity of successive segments appears relatively uncoordinated. During this type of backward movement the posterior abdomen is flexed dorsally. These two methods of backward locomotion often occur in sequence, with the peristaltic backing occurring directly after the initial withdrawal and the gliding walk following thereafter when the worm lies deeper in its tube.

Forward locomotion and twisting of the body

—Forward locomotion in the tube is carried out by a mechanism best described as "walking." The posterolaterally directed parathoracic palae push against the tube wall and thrust out of their setal sacs, exerting a forward force on the body. A worm withdraws the rear of the tube retracts its tori, losing lateral contact with the tube wall, and moves forward by paleal thrusts.



shortened its body in an initial withdrawal response likewise re-extends anteriorly by paleal walking rather than by forceful forward muscular extension. This activity of setal extension appears nonmetameric.

Body twisting (Fig. 1a), is accomplished by the action of the parathoracic neurosetae. These setal bundles are directed toward the mid-line ventrally, and when those of only one side are forcefully extended against the tube wall, a torque is exerted about the body axis in a direction opposite to the thrust. Twisting often occurs in conjunction with forward locomotion. The neurosetae can also twist the anterior body while the worm is in a stationary position, but not to the degree that occurs during forward movement.

Ciliary currents within the tube.—The ciliary currents associated with feeding in *Phragmatopoma* have been observed by Dales (1952), but the currents within the tube were not described. Observations both on active worms within their tubes and on relaxed animals removed from their tubes show the major ciliary tracts responsible for water circulation within the tube to be as follows:

(1) Discrete transverse bands of cilia are present along the entire dorsal surface of the abdomen, thorax, and opercular stalk (Figs. 3b and 4b). The beat of these cilia moves water anteriorly.

(2) The dorsal cirri of the thorax and abdomen also bear transverse ciliated ridges on their medial surfaces. The bands are reduced posteriorly along with the reduction in size of the cirri. The dorsal cirri are normally directed anteromedially (Figs. 1a, b), hence their cilia move water anteriorly in the space between the dorsal body wall and the adjacent inner surface of the tube.

(3) The lateral body wall between successive parapodia bears numerous longitudinally oriented bands of cilia. These bands are most extensive on the anterior abdominal region (Fig. 4a) and are reduced posteriorly as the notopodial tori become narrower and more elongate.

No ciliary action was observed on the parapodia themselves. At the anterior end of the body, the opercular stalk also bears longitudinal

bands of cilia on its lateral surface. These move water toward the dorsum (Fig. 4c).

The ventral surfaces of the thorax, abdomen, and the entire cauda are devoid of ciliary bands. The ventral surface of the opercular stalk bears transverse bands of cilia which beat anteriorly and function in the rejection of particles from the mouth (Fig. 4c).

The bracing of the body in a central position along the axis of the tube by the tori provides space all around the body for water circulation. Figure 2a shows the general circulation pattern. When a worm is in an expanded condition with its head at the aperture of the tube, water is drawn into the tube past the ventral surfaces of the head and thorax. Some water is passed dorsally by the lateral cilia of the opercular stalk and the interpodial thoracic cilia (Fig. 3a) but most of it flows posteriorly along the channel beneath the abdomen. The beat of the interpodial cilia moves water dorsally between successive tori all along the abdomen (Fig. 4a). These segmentally separated streams join the main dorsal current which flows anteriorly and is powered by the cilia of the dorsum and the dorsal cirri. Figure 4b illustrates the interpodial and dorsal currents and the manner in which the interpodial ciliary bands merge with those of the dorsum. The dorsal exhalent current passes out over the dorsal surface of the opercular stalk (Fig. 3b). Gametes have been observed emerging from the tube in the dorsal current during spawning.

An eddy exists in the water around the head of expanded worms. Figure 3a illustrates how the interaction of the dorsal exhalent current, the ventral inhalent current and the rejection current from the ventrum of the opercular stalk combine to produce this eddy. This phenomenon may facilitate the collection of particulate matter by the feeding tentacles of the head.

Thoracic pumping.—*Phragmatopoma californica* exhibits a peristaltic pumping behavior when it is withdrawn in its tube. This behavior always occurs in withdrawn worms, whether they are only slightly withdrawn into the tube opening or deeply placed in the tube. Pumping is accomplished by a piston-like peristalsis confined to the parathoracic region. Presumably this behav-

Figure 4. Somites of the anterior abdominal region of *Phragmatopoma californica*, showing the position of the ciliary bands. a. Ventral views. b. Lateral view from the right side. c. Lateral view with the cirri of the right side removed. See figure 1 for key to abbreviations.

serves to increase the rate of water exchange at the mouth of the tube when the worm is withdrawn.

During pumping, the parathorax shortens and broadens, contacting the tube wall. The thorax is pushed anteriorly on the forward stroke by a single extension of the parathoracic palae. Then the parathorax constricts, losing its contact, and is retracted by a short longitudinal contraction. A complete pumping stroke is repeated 40 to 60 times a minute.

Defecation and fecal elimination.—The cauda of *P. californica* does not extend forward more than one half the length of the abdomen of an expanded worm. Even in a contracted worm, the cauda has not been seen to extend anteriorly beyond the anterior end of the abdomen. The anus at the tip of the cauda lies in a mid-ventral position, facing into the ventral inhalent current.

Feces are extruded from the anus in the form of continuous strings. The extrusion is accomplished by peristaltic waves that begin at the anus and travel up the cauda to its origin at the abdomen. The abdominal neurosetae commence anteriorly directed stroking or rowing motions during defecation. These motions do not appear metameric. Nevertheless, the opposed tips of the neurosetae on the two sides of the body grasp the fecal string, and actually pull it out of the anus as it is extruded. The fecal matter is broken into 3 to 5 mm lengths during this process and is passed anteriorly to the posterior margin of the ventral plate. The animal then undergoes a withdrawal-like response which expels the feces ventrally from the tube.

DISCUSSION

Previous studies of sabellariid behavior have been carried out largely on other species, but have been limited as normal behavior of the worms could not be observed *in situ*. Nevertheless, findings of earlier workers often agree with present observations on *Phragmatopoma californica*. Since there are close morphological similarities among the Sabellariidae, it is logical to assume that the behavior of *P. californica* may be considered generally representative for the family.

The use of uncini or uncinigerous tori as a means of maintaining position within the tube is widespread within the Sedentaria. *Phragmatopoma californica*, and presumably other sabellariids, have developed this to a high degree.

The extended tori are situated so that water circulation can take place freely around the body. Watson (*in* McIntosh, 1922) observed that the posterior tori of *S. alveolata* could . . . "be moved freely backward and forward, as well as retracted," but he did not determine their locomotory function.

Although there was no mention of the twisted posture so often seen in *P. californica*, Watson (*in* McIntosh, 1922) did deduce the functions of the parathoracic palae and neurosetae in *S. spinulosa* which could result in body rotation. Kirtley (1968) alludes to the locomotory function of the parathoracic palae of *P. lapidosa*, but included no details. He also assigned a locomotory function to the abdominal neurosetae in that species which has not been observed in *P. californica*.

Watson (*in* McIntosh, 1922) suggested that the parathoracic palae of *S. spinulosa* are involved in the shaping of the tube and Kirtley (1968) reported the same for *P. lapidosa*. The only observed uses of the thoracic palae by *P. californica* have been bracing the body, locomotion, and pumping.

According to Kirtley (1968), *P. lapidosa* uses its opercular palae for grasping and manipulating sand grains during tube building. This behavior was not observed in *P. californica* during tube building in the petri dishes. Manipulation and positioning of the sand grains was accomplished by the building organ of *P. californica* in a manner similar to that shown by Vovelle (1965) for *S. alveolata*.

Some previous workers have commented on the presence of cilia or on water currents about the bodies of sabellariids. Watson (*in* McIntosh, 1922) and Kaestner (1967) both noted the existence of a main exhalent dorsal current. Watson (*in* McIntosh, 1922) suggested that rowing motions of the abdominal neurosetae in *S. spinulosa* helped to create water currents, and that water was expelled from the tube anteriorly by undulatory movements of the body. Kirtley (1968) reported that in expanded specimens of *P. lapidosa*, currents in and around the tube were aided by "peristaltic motion of the body segments." In *P. californica* circulation of water and expulsion of water from the tube were normally carried out by ciliary action; expulsion of water by body movement occurred only during pumping, withdrawal, and fecal elimination. Moreover, peristaltic thoracic pumping occurred only while the animal was withdrawn.

Several workers have commented on the position of the cauda and the matter of defecation in different sabellariids. Watson (*in* McIntosh, 1922) suggested that the abdominal neurosetae hold the cauda in position. This is not the case in *P. californica*, where the cauda lies freely under the abdomen; the neurosetae normally touch it only during defecation. In *S. alveolata* Watson (*in* McIntosh, 1922) "also noticed in a young example the ejecta discharged from the gut in a thread-like form and worked forward by ciliary action and perhaps the movement of the bristles. The annelid then protruded its anterior region, and with a sudden jerk inward the refuse was dropped outside the tube." Wilson (1969) indicated that defecation in *S. alveolata* takes place by the extension of the cauda forward so that the anus is protruded out of the tube mouth. This was never observed in *P. californica*. Kirtley (1968) stated that the abdominal neurosetae of *P. lapidosa* were responsible for "removing metabolic wastes from the tube," but does not report how this is done. Kaestner (1967) stated that the dorsal exhalent current carries feces out of the tube, which was never seen in *P. californica*.

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THE SYSTEMATICS AND DISTRIBUTION OF MARINE TUBIFICIDAE
(ANNELIDA: OLIGOCHAETA) IN THE BAHIA DE SAN QUINTIN,
BAJA CALIFORNIA, WITH DESCRIPTIONS OF
FIVE NEW SPECIES

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ABSTRACT: Marine Tubificidae (Annelida, Oligochaeta) from Bahía de San Quintin, Baja California, are described, and their distribution in the bay noted relative to the mean particle size of the sediments. *Tubifex postcapillatus*, n. sp. is characterized by its simple-pointed dorsal setae, and short hair setae which occur in postclitellar segments only. The setal pattern and details of the genital anatomy distinguish *Thalassodrilus belli*, n. sp. from other members of its genus. Both of these species are associated with the finest sediments which are located mainly at the north end of the bay. *Limnodriloides monothecus*, n. sp. with its single, mid-dorsal spermatheca unique to this genus, occurs mainly in silts and very fine sands (4 to 5 ϕ). *Limnodriloides verrucosus*, n. sp. possesses a papillate body wall previously unknown in the genus, but reminiscent of the *Pelosclex* condition; it occurs in all sediment types in the bay (3 to 8 ϕ) but is most abundant in the 5 to 6 ϕ range. The dominant oligochaete, *Limnodriloides barnardi*, n. sp., closely resembles *Limnodriloides winckelmanni* Michaelsen, especially in its possession of elongate, grooved spermathecal setae enclosed in vacuolated sacs; the species are distinguished by details of their penial structures. *Limnodriloides barnardi*, n. sp. occurs in all sediment classes but its optimum range appears to be in 4 to 6 ϕ sediments.

In a general report on the benthic exploration of Bahía de San Quintin, Baja California, in 1960–1961, Barnard (1962) pointed out that unpolluted or unmodified bays and enclosures of the Southern Pacific region of North America are both rare and poorly known biologically. Barnard (op. cit.) states the two primary objectives of the survey as “. . . a search for basic information on an unpolluted enclosure as near southern California as possible, and the initiation of comparative investigations planned by the Institute of Marine Bio-Research on many such enclosures in the Eastern Pacific.” This paper reports on the systematics and distribution within Bahía de San Quintin of the tubificid oligochaetes.

The recognition of Oligochaeta, mainly Tubificidae, as regular components of the marine benthic community, has occurred only within the last decade. Previously oligochaetes were regarded as more or less exclusively fresh-water or terrestrial with an occasional species “invading” the marine environment via estuaries and fresh-water sources in the littoral zone. Undoubtedly this may be true of some species, but the works of Brinkhurst (1963; 1966), Hrabě (1966; 1967; 1971a; 1971b), and Cook (1969; 1970a; 1971) have demonstrated that a significant number of truly marine Tubificidae exist, including some from the deep sea (Cook, 1970b).

The collection of Tubificidae from Bahía de San Quintin, numbering 55 samples, each containing from 1 to about 500 worms, was received for examination from the Smithsonian Institution. Five species of Tubificidae have been recognized, namely, *Tubifex postcapillatus* n. sp., *Thalassodrilus belli* n. sp., *Limnodriloides barnardi* n. sp., *Limnodriloides monothecus* n. sp., and *Limnodriloides verrucosus* n. sp.

STUDY AREA AND METHODS

Bahía de San Quintin is located on the Pacific side of Baja California with its northeastern tip at 30° 30' N, 116° 00' W. A full description of the study area, field, and laboratory methods, involved in the survey is available in Barnard (1962). Briefly, an area of six square miles in the eastern arm of the bay was sampled as uniformly as possible at a density of 15 stations per square mile. A benthic sample was collected at each station (designated SQ 1 to 94) using a

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modified Hayward orange-peel grab with a capacity of 650 sq cm (0.065 sq cm). Material from the grab was washed through a Tyler screen (12.6 mesh strands per cm; mesh diameter 0.495 mm), the animals preserved in 4 percent formalin and transported to the laboratory. Here they were rewashed through a screen (23.6 mesh strands per cm), sorted into taxonomic groups, stored in formalin for three months and finally transferred to 70 percent ethanol.

The Oligochaeta had been lightly stained in eosin, dehydrated, and transferred to methyl salicylate by the late A. W. Bell, who had also made microscope slide preparations of one to four individuals from a number of samples; from this preliminary survey Bell had apparently recognized the presence of a *Limnodriloides* (some slides labelled as "*L. winckelmanni*") and a species of "*Peloscolex*" or "*Tubifex*" (= *T. postcapillatus*). After Bell's slides had been examined to assess the number and type of taxa involved, material in fluid was studied and identified using: a) temporary mounts in methyl salicylate; b) permanent whole mounts in Canada Balsam, stained in eosin; c) permanent mounts of dissected worms lightly stained in either eosin or Harris' haematoxylin. In 25 samples the numbers of worms were too large to permit identification of every individual, therefore subsamples of about 30 worms were taken by the following method which eliminates, or minimizes, any selection bias for large individuals. Material was transferred to a small dish where it was spread out uniformly (as estimated visually): 30 individuals were separated from one small area (size dependent on total sample size) and these identified. A rough estimate of the total number of individuals (T) in these samples was arrived at by comparing the area occupied by 30 individuals (As) with the total area of the sample dish (At); i.e., $T = 30 (At)/As$.

SYSTEMATIC ACCOUNTS

Tubifex postcapillatus, new species

Figure 1

Holotype.—United States National Museum (USNM) catalogue number 45289. Bahia de San Quintin. Station number SQ 1. Depth, less than 2 m, in gray clay. Collected 22 April 1960.

Paratypes.—USNM 45290. Five individuals from SQ 9 (less than 2 m depth, in black sandy silt with small amounts of clay; collected 22 April 1960), and four individuals from SQ 5 (less than 2 m depth,

in dark grey silt; collected 22 April 1960). Museum of Natural Sciences, Ottawa (USNM catalogue number 3475. One individual, holotype.

Etymology.—"capillatus" = L. "long-haired"; hence species has hair setae posteriorly.

Description.—Up to 58 segments, 1.25 mm long. Diameter 0.24 to 0.41 mm anteriorly, 0.33 mm at segment XI, 0.33 mm tapering to a minimum of 0.16 mm posteriorly. Prostomium rounded as long as, or shorter than it is wide at the peristomium junction. Clitellum weakly developed on segment XI and ½ XII. Dorsal setae: in segments II to X each bundle contains 3 to 4, sometimes 5, bifid setae 75 to 85 μ long, with the upper tooth slightly longer than the lower; from about segment XIII to terminal segment each bundle contains two or three smooth hair setae 110 to 125 μ long, and two or three elongate, single-pointed crochets 80 to 95 μ long; modified crochets and hair setae are similar in appearance but differ in the latter's lack of a node, more slender form, and greater length. Ventral setae: anteriorly each bundle contains three to five bifid setae 70 to 88 μ long, with the upper tooth slightly longer than the lower; posteriorly each bundle has two setae similar in form and length to anterior setae. No modified genital setae. Paired spermathecal and male pores are situated in the line of the ventral setae on segments X and XI respectively.

Male genital system (all structures paired): vas deferens 25 to 31 μ diameter, about 1.25 mm long (in holotype), joins the atrium subapically and dorsally, opposite to the prostate gland. Atria hook—to comma-shaped, reflexed posteriorly, about 340 μ in total length, 54 to 100 μ diameter; atria reach their maximum diameter distally to vas deferens prostate junctions; internal lining epithelium of this swelling more glandular than remaining atrial lining. Atria terminate in cuticularized penes 105 to 135 μ long, 50 to 70 μ diameter. Prostate gland relatively small, more or less enclosed by "hook" of atrium. Paired spermathecae with large ovoid to sacciform ampullae and barrel-shaped ducts about 135 μ long, 60 μ diameter. Spermatozoegmata elongated ovoids, about 260 μ long, 63 μ maximum diameter.

Remarks.—*Tubifex postcapillatus* differs from other members of the genus in possessing hair setae and simple-pointed crochets only in posterior segments. In other species, where they occur, hair setae are always present in, and tend to be more numerous on, anterior segments. Simple-pointed posterior setae are known in some *Peloscolex* species [e.g., *P. heterochaetus* (Malmgren, 1926), *P. swirencovi* (Jaroschewicz, 1969) and *P. intermedius* Cook, 1969] but this genus is characterized by the possession of a papillate or ridged body wall, at least at some time in its life cycle: the distinctions between 7

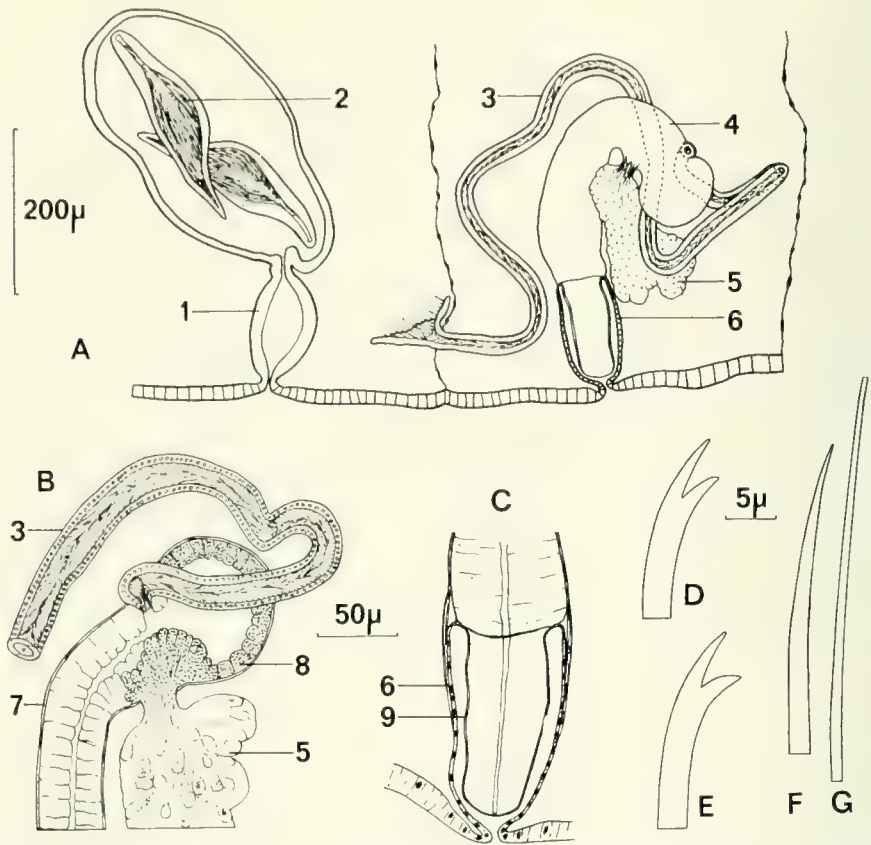


Figure 1. *Tubifex postcapillatus*, n. sp. A, Longitudinal view of genital segments; B, Distal end of atrium (optical section); C, Penis; D, Anterior dorsal seta; E, Anterior ventral seta; F, Posterior dorsal crochet; G, Part of hair seta (same bundle as F). 1, spermathecal duct; 2, spermatozeugma; 3, vas deferens; 4, atrial ampulla; 5, prostate gland; 6, penial sac; 7, atrial muscle layer; 8, glandular epithelium of distal atrium; 9, penial sheath.

Peloscolex, which are complex and probably artificial, are discussed in Pickavance and Cook (1971). Immature, semi-mature and mature individuals of *T. postcapillatus* which were examined showed no trace of papillation, body wall ridges or accumulations of foreign particles, and is therefore precluded from *Peloscolex* as this is presently defined.

Thalassodrilus Brinkhurst, 1963

Definition.—Hair setae absent. Penial setae present or absent. Body wall smooth. No gut diverticulae. Thick muscle layer associated with paired atria, at least terminally. Wide vasa deferentia, shorter than, or about as long as the atria, enter the latter apically. Each atrium with a small compact prostate gland. Spermathecae small or absent. Sperm in spermathecae in random masses; spermatozeugmata absent. Coelomocytes absent.

Type species.—*Rhyacodrilus prostates* Knöllner, 1935.

Remarks.—*Thalassodrilus* was established by Brinkhurst (1963) to accommodate *R. prostates*. Hrabě (1967) rejected the genus and placed *R. prostates* in *Limnodriloides* but later (Hrabě, 1971b) modified his opinion, redefined *Thalassodrilus*, and included in it *R. prostates*, *Limnodriloides roseus* Pierantoni, 1903, *Limnodriloides pectinatus* Pierantoni, 1903, and *Limnodriloides gurwitschi* Hrabě, 1971 (1971a). The modified definition of *Thalassodrilus* given above differs from Brinkhurst's (1963) and Hrabě's (1971b) conception of the genus by its specific reference to the heavy musculature associated with the male genitalia, and contains *T. prostates* (Knöllner), *T. gurwitschi* (Hrabě) and *T. belli*, n. sp. The descriptions of *L. roseus* and *L. pectinatus* are in-

adequate and in this author's opinion should remain as species inquirendae in *Spiridion* (Cook, 1969; Brinkhurst and Jamieson, 1971); they cannot be included in either *Limnodriloides* because they lack gut diverticulae, or *Thalassodrilus* because they do not possess heavy atrial or pseudopenial musculature.

Some problems with *Thalassodrilus* do remain however. *Thalassodrilus gurwitschi* and *T. belli* are clearly closely related and, except for their lack of gut diverticulae and possession of relatively wide vasa deferentia, could be considered as species of *Limnodriloides*; both differ from *T. prostatus* in their common possession of thick muscular pseudopenes and distinct thin-walled atria, rather than the thick, muscular, pear-shaped structures thought to be the atria in *T. prostatus*. It is argued that the latter could be derived from a *T. gurwitschi*-like ancestor by the excessive or precocious development of the pseudopenial musculature which finally enveloped and incorporated the original atrium both morphologically and functionally. The author feels that because of this possible mechanism together with the possession of relatively wide vasa deferentia and the other, mainly negative, characters included in the generic definition, the three species here included in *Thalassodrilus* form a convenient, and possibly monophyletic group. An additional advantage of the arrangement is the removal of *T. gurwitschi* (and *T. belli*) from *Limnodriloides* which therefore remains the homogenous taxon defined in Cook (1969) (and see discussion under *Limnodriloides*, below).

KEY TO SPECIES OF *THALASSODRILUS*

- 1a. Penial setae present. Atria pear-shaped with thick muscular walls *T. prostatus* (Knöllner)
- b. Penial setae absent. Atria elongate, thin-walled, with muscular pseudopenes terminally 2
- 2a. Spermathecae present *T. belli*, n. sp.
- b. Spermathecae absent *T. gurwitschi* (Hrabě)

Thalassodrilus belli, new species

Figure 2

Holotype.—USNM 45287. Bahia de San Quintin, Station SQ 3. Depth, less than 2 m, in gray clay. Collected 22 April 1960.

Paratypes.—USNM 45288. One individual from SQ 1 (in black mud); four individuals from SQ 2 (in dark gray clay); one individual from SQ 6 (very dark clay, some lighter clay); one individual from SQ 7 (black sandy silt); for all stations depth,

less than 2 m; collected 22 April 1960.

One individual from SQ 5. Depth, less than 2 m, in dark gray silt. Collected 22 April 1960.

Etymology.—The species is named in honor of the late Dr. A. W. Bell who began the collection of this collection.

Description.—55 to 63 segments. 13 mm long. 0.32 to 0.43 mm diameter anteriorly, 0.4 to 0.61 mm at segment XI, 0.4 mm tapering to 0.2 mm posteriorly. Prostomium shorter than it is wide at the peristomium junction. Clitellum restricted to segment XI and a small part of segment XII. Dorsal and ventral setae similar in number, size and shape: setae three to five per bundle anteriorly, two per bundle posteriorly; setae bifid, 69 to 105 μ long, with the upper tooth slightly thinner than, but as long as, the lower; setae in the middle region of the body tend to be shorter than others. Paired male and spermathecal pores open in the line of the ventral setae; spermathecal pores open near intersegmental furrow IX/X.

Pharyngeal glands in segments IV and V. Chloragogen cells begin in segment VI. No discernable gut diverticulae. Male genital system (all structures paired): vas deferens, about 265 μ long, 20 to 30 μ diameter, joins atrium apically. Atrium about 335 μ long, with an apical swelling 47 to 54 μ diameter, and a long duct 20 to 26 μ diameter which is convoluted or folded proximally. Folded part is enclosed in a muscular sac, forming a protrusible pseudopenis. Prostate gland small, joined to the atrial swelling ventrally. Paired spermathecae relatively very small, pear-shaped, 70 to 110 μ diameter with very short, indistinctly separated ducts. Sperm in spermathecae in random masses.

Remarks.—The general dimensions, the peculiar form of the male genitalia, the number and form of the setae, and the absence of gut diverticulae, are all characters similar in, or common to, both *T. belli* and *T. gurwitschi*. The latter species, however, has no trace of spermathecae in the many mature and immature individuals studied by Hrabě (1971a; pers. comm.). A further distinction between the two species is found in the setae; in *T. gurwitschi* the upper tooth of each seta is distinctly thinner at the base than the lower tooth (Hrabě, 1971a, Fig. 1 a-c) whereas in *T. belli* the basal width of the teeth are approximately equal (Fig. 2d).

Limnodriloides Pierantoni, 1903

Definition.—Hair setae absent; somatic setae all bifid crochets. Penial setae absent. Body wall smooth or, rarely, with raised papillae. Gut in immediate preclitellar region with a pair of diverticulae. Paired atria divisible into well-defined ampullae and duct regions, both with relatively thin muscle walls. Vasa

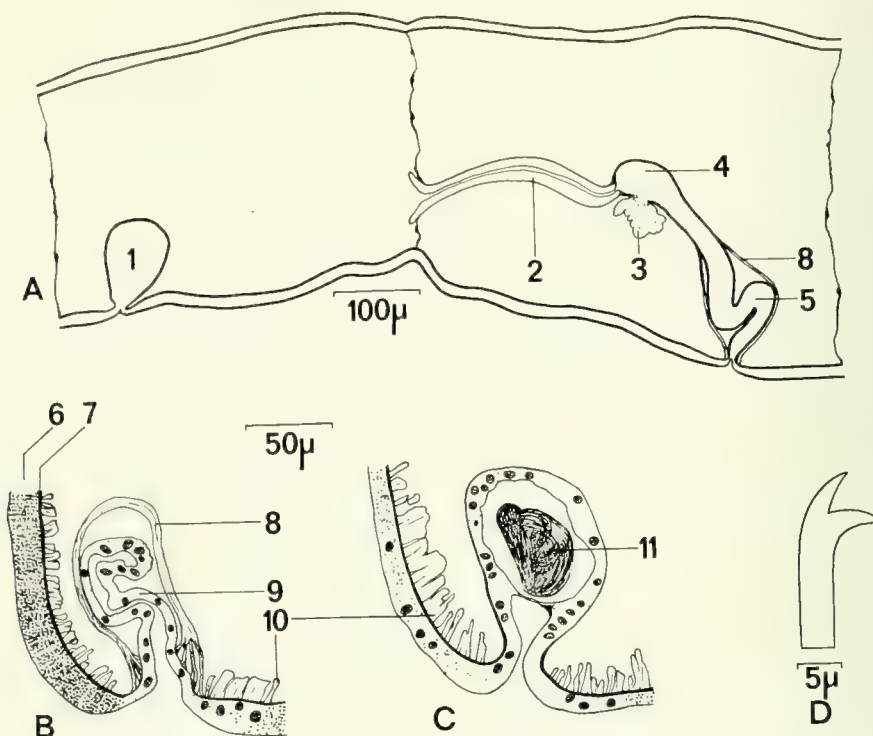


Figure 2. *Thalassodrillus belli*, n. sp. A, Longitudinal view of genital segments; B, Transverse section of male pore; C, Transverse section of spermatheca; D, Seta (segment VIII). 1, spermatheca; 2, vas deferens; 3, prostate gland; 4, atrial ampulla; 5, penial complex; 6, epithelium of clitellum; 7, circular muscle; 8, muscle sac surrounding penis; 9, lining epithelium of penial duct; 10, longitudinal muscle; 11, sperm mass.

deferentia about as long as, or slightly longer than, the atrial ampullae (excluding the duct) which they join more or less apically. Compact prostate glands join atria on discrete, broad prostatic ducts. Penial structures variable in form but are rarely absent. Spermathecae relatively large. Spermatzeugmata absent, but in most species sperm in the spermathecae are organized into discrete, oriented bundles. Coelomocytes absent.

Type species.—*Limnodriloides appendiculatus* Pierantoni, 1903.

Remarks.—A short history of *Limnodriloides*, a revised diagnosis of the genus, and reasons for removing *S. roseus* (Pierantoni) and *S. pectinatus* (Pierantoni) from it, are given in Cook (1969) (also *vide supra* under *Thalassodrillus*). Briefly, the presence of the unique gut diverticulae found in the eighth or ninth segment is considered as the positive unifying somatic character of *Limnodriloides*. Hrabě (1971b) apparently accepted this proposition but, on the basis of the structure of the intromittent organs, split the genus into two; he restricted *Limnodriloides* to

those species possessing pseudopenes (containing *L. appendiculatus*, *L. agnes*, Hrabě, 1967, and *L. winckelmanni* Michaelsen, 1914) and established *Bohadschia* for the species with true penes (containing *L. medioporus* Cook, 1969, *B. maslinicensis* Hrabě, 1971, and *B. pierantonii* Hrabě, 1971). In this paper three new species are described; *L. monothecus* and *L. verrucosus* which both possess pseudopenes (*i.e.* *Limnodriloides sensu* Hrabě) and *L. barnardi* which has complex intromittent organs showing characteristics of both pseudopenes and true penes (see remarks following the description of this species). Because of this intermediate type and because *L. barnardi* appears to be very close to *L. winckelmanni*, the distinction between Hrabě's *Limnodriloides* and *Bohadschia* can no longer be considered valid, even at the subgeneric level, therefore Cook's (1969) conception of *Limnodriloides* is retained in this account.

Limnodriloides monothecus is analogous to *P. monospermathecus* (Knöllner, 1935) in *Phallo-drillus*; in both cases the possession of a single

dorsal spermatheca, rather than paired ventral ones, is considered to be significant at the species level only. However, the organization of the sperm in the spermatheca of *L. monotheucus*, and other members of the genus, needs closer examination.

In *L. appendiculatus*, *L. agnes*, and *L. medioporus*, the sperm is arranged in the spermathecae in oriented bundles (Hrabě, 1967; Cook, 1969); in *L. winckelmanni* and *L. barnardi* the sperm bundles are more regular in form than those of the three former species (Michaelsen, 1914; Hrabě, 1967; *vide infra*); both Michaelsen and Hrabě (op. cit.) refer to these structures as spermatophores or spermatozuigmata in *L. winckelmanni*, and Hrabě (1967) is unable to decide whether the sperm bundles of *L. agnes* are spermatozuigmata or not. Observation of the sperm bundles of *L. medioporus* and *L. barnardi* has shown that the sperm tails tend to be organized into parallel bundles, some of which appear to have coalesced or adhered closely to each other. The orientation of sperm is developed to a higher degree in *L. monotheucus*; in this species the sperm bundles are very long and narrow with the sperm heads (darkly staining in haematoxylin) concentrated at one end of the bundle, and the sperm tails, arranged in very loose spirals, composing the remaining two-thirds of the bundle (Fig. 4b). The term "spermatozuigma" is used in the Tubificidae to denote a sperm aggregation in which sperm heads occur around a central axis with the sperm tails, which are embedded in a cementing substance, radiating from this axis in a spiral manner (Stephenson, 1930; Brinkhurst and Jamieson, 1971). The sperm bundles of *Limnodriloides*, including the highly organized bundles of *L. monotheucus* cannot therefore be considered as spermatozuigmata.

A character which has been added to the generic diagnosis of *Limnodriloides* is the nature of the body wall. This is necessary because of the discovery of *L. verrucosus* which, although clearly a *Limnodriloides* (form of the male genitalia and presence of gut diverticulae) has a papillate body wall superficially indistinguishable from that of many species of *Peloscoclex* (see also remarks following the description of *L. verrucosus*).

KEY TO SPECIES OF LIMNODRILOIDES

- 1a. One pair long, hollow-ended spermathecal setae, each contained in large muscle-coated sac, situated on segment X. Atrial duct lined, at least in part, with glandular epithelium 2

- b. Modified spermathecal without glandular lining epithelium
- 2a. Intromittent organs small, penes surrounding ends of spermathecal than setal shaft *L. winckelmanni* Mi
- b. Intromittent organs large penes (in part) in voluminous penial sacs. Muscle surrounding ends of spermathecal setae about as thick as shaft *L. barnardi*, n. sp.
- 3a. Single, elongate, carrot-shaped spermatheca present, opening mid-dorsally *L. monotheucus*, n. sp.
- b. Spermathecae paired, opening ventrally or ventro-laterally 4
- 4a. Body wall papillate, at least in postclitellar region *L. verrucosus*, n. sp.
- b. Body wall smooth 5
- 5a. In posterior segments setae one per bundle. Atrial duct at least as long as vas deferens *L. agnes* Hrabě.
- b. In posterior segments setae two per bundle. Atrial duct shorter than vas deferens 6
- 6a. Genital pores contained in median ventral folds in body wall, appearing externally as elongate median slits arranged transversely *L. medioporus* Cook.
- b. Genital pores paired, ventro-lateral 7
- 7a. Gut diverticulae in segment VIII *L. appendiculatus* Pierantoni.
- b. Gut diverticulae in segment IX 8
- 8a. In preclitellar segments setae two per bundle. Vasa deferentia 9 to 13 μ wide. Terminal part of male ducts S-shaped *L. maslinicensis* (Hrabě).
- b. In preclitellar segments setae usually three per bundle. Vasa deferentia 16 μ wide. Terminal part of male ducts straight *L. pierantonii* (Hrabě).

Limnodriloides monotheucus, new species

Figure 3

Holotype.—USNM 45285. Bahia de San Quintin, station SQ 16. Depth, less than 2 m. in dark grey sandy silt. Collected 23 April 1960.

Paratypes.—USNM 45286. Six individuals, data as for holotype; one individual from SQ 37 (Depth, less than 2 m. in grey silt, collected 24 April 1960). NMC 3478. One individual from SQ 9 (Depth, less than 2 m. in black sandy silt with small amounts of clay, collected 22 April 1960).

Etymology.—"mono" = Gr. "one, single"; "theuca" = Gr. and L. "case, receptacle"; hence "single spermatheca."

Description.—About 46 segments, 9.5 mm long 0.12 to 0.23 mm diameter anteriorly, 0.27 mm at segment XI, 0.23 tapering to 0.13 mm posteriorly. Prostomium rounded, shorter than it is wide at the peristomium junction. Clitellum very weakly developed or indiscernable. Dorsal and ven-

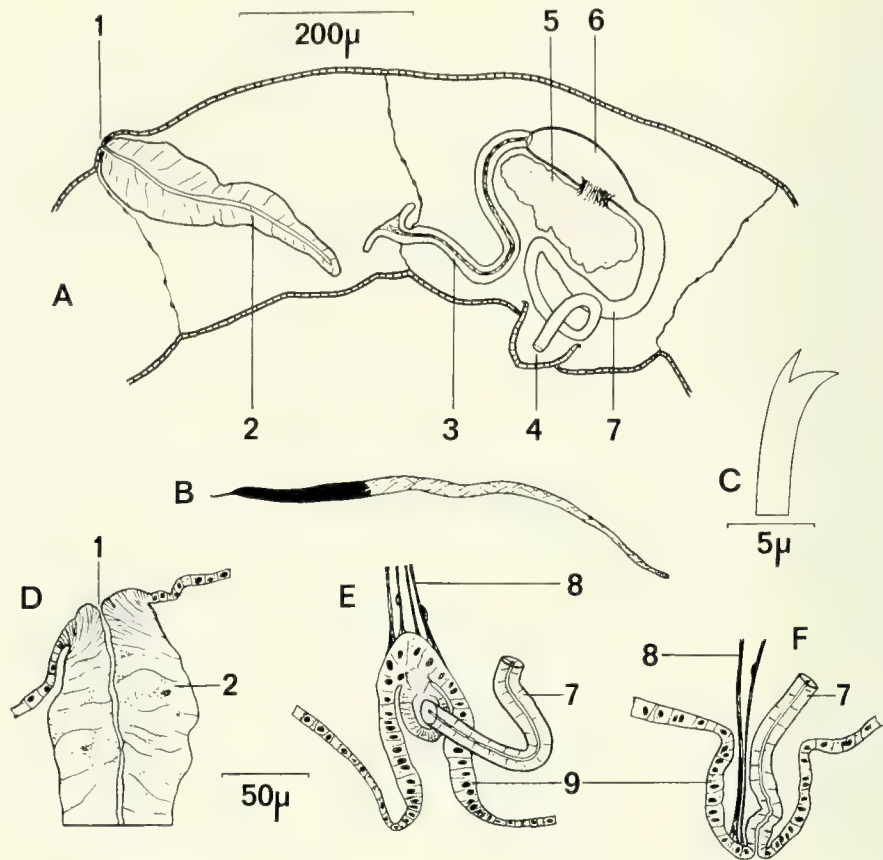


Figure 3. *Limnodriloides monotheclus*, n. sp. A, Longitudinal view of genital segments; B, Sperm bundle; C, Somatic seta; D, Proximal end of spermatheca; E, Penis sac (resting position); F, Penis sac (everted position). 1, spermathecal pore; 2, spermatheca; 3, vas deferens; 4, male pore; 5, prostate gland; 6, atrial ampulla; 7, atrial duct; 8, penis retractor muscles; 9, penis sac epithelium.

tral setae similar in number, size and shape: setae 3, sometimes two per bundle in segments II to IX, absent in X and XI, and two per bundle from segment XII to terminal segment; setae bifid, 40 to 50 μ long, with upper tooth shorter and thinner than the lower. No modified genital setae. A single mid-dorsal spermathecal pore is situated near intersegmental furrow IX/X. Male pores paired, ventrolateral.

Pharyngeal glands present in segments IV and V. A pair of diverticulae join the gut in the middle of segment IX. Male genital system (all structures paired): relatively thick vas deferens, 23 to 34 μ diameter, 245 to 300 μ long, joins atrium more or less apically. Atrium consists of an ovoid ampulla, 90 to 130 μ long, 35 to 50 μ diameter, and an elongate, tubular duct 450 to 550 μ long, 13 to 27 μ diameter, which opens to the exterior in an evaginable sac from the median side; sacs 90 to 105 μ long, 60 to 77 μ maximum diameter when evaginated. Prostate gland joins atrium ventrally, near to the ampulla/

duct junction. Single median spermatheca elongate, carrot-shaped, 280 to 400 μ long, 55 to 85 μ maximum diameter, tapering to about 20 μ distally. Sperm in spermatheca oriented into long narrow bundles 200 to 260 μ long, 6.8 μ maximum diameter, with the darkly staining sperm heads all occurring at one end of the bundle.

Remarks.—The single, mid-dorsal spermatheca found in *L. monotheclus*, though unique in *Limnodriloides*, is also known in *Phallodrilus monospermatheclus*.

Limnodriloides verrucosus, new species

Figure 4

Holotype.—USNM 45283. Bahia de San Quintín, station SQ 41. Depth, less than 2 m, in gray very fine sandy silt. Collected 24 April 1960.

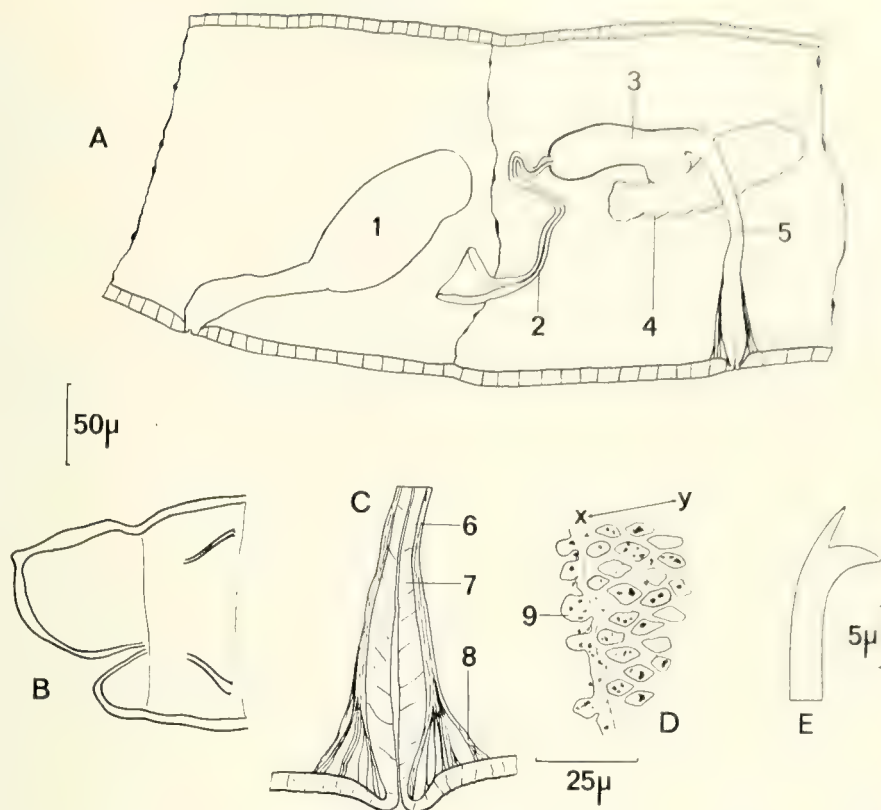


Figure 4. *Limnodriloides verrucosus*, n. sp. A, Longitudinal view of genital segments; B, Prostomium and first two segments; C, Penis; D, Body wall of posterior segment (x - y = transverse axis of body); E, Somatic seta. 1, spermathecal ampulla; 2, vas deferens; 3, atrial ampulla; 4, prostate gland; 5, atrial duct; 6, circular muscle layer of atrial duct; 7, atrial duct lining epithelium; 8, penis protractor muscle; 9, body wall papilla.

Paratypes.—USNM 45284. One individual from SQ 39 (in gray very fine sand; collected 23 April 1960); three individuals from SQ 46 (in gray silty very fine sand; collected 24 April 1960); two individuals from SQ 49 (in gray very fine silty sand; collected 24 April 1960); two individuals from SQ 58 (in gray silty very fine sand; collected 24 April 1960). NMC 3476. One individual from SQ 54 (in gray silty fine sand; collected 24 April 1960). Depths (all paratypes), less than 2 m.

Etymology.—"verrucosus" = L. "warty."

Description.—Up to 45 segments. 7.5 to 13 mm long. 0.12 to 0.18 mm diameter anteriorly, 0.18 to 0.25 mm at segment XI, 0.17 tapering to 0.08 mm posteriorly. Prostomium a little shorter than it is wide at the peristomium junction, with a small, thin-walled papilla anteriorly. Body wall covered with a sparse to very dense layer of raised papillae and small foreign particles, usually beginning just behind the clitellum in mature individuals, but occurring in anterior segments of immature specimens. Clitellum confined to segments XI and a small part of XII.

Dorsal and ventral setae similar in number, size and shape: setae two per bundle in segments II to VII and one per bundle from VIII to the terminal segment; setae absent on segments X and XI (no modified genital setae); all setae bifid, 40 to 65 μ long, with the upper tooth thinner than, but about as long as the lower. Male and spermathecal pores paired in the line of the ventral setae.

Pharyngeal glands in segments IV and V. A pair of diverticulae join the gut ventro-laterally in the middle region of segment IX and extend anterior to septum VIII IX. Male genitalia (all structures paired): vas deferens, 7.3 to 10.5 μ diameter and about as long as, or slightly shorter than the atrium, join latter apically. Atrium thin, elongate, with a thickly stalked prostate gland joining its ampulla ventrally on a raised papilla. Atrium with a cylindrical ampulla about 100 μ long, 13.7 to 35 μ diameter, and a tubular duct 8 to 11.5 μ diameter swelling to about 21 μ terminally; total length of atrium about 220 μ . Long axis of atrium directed anteriorly. Muscles from swollen end of atrial duct join body

wall, forming a protrusible pseudopenis. Paired spermathecae with ovoid to elongate ampullae 97 to 113 μ long, 48 to 57 μ wide, and discrete ducts 57 to 73 μ long, 14 to 19 μ diameter. Sperm in spermathecae in random masses (no trace of oriented bundles).

Remarks.—The papillate body wall of *L. verrucosus* is unique in *Limnodriloides*, but is morphologically indistinguishable from the condition found in many *Peloscolex* species. In the latter genus wide intraspecific variation of the nature of the body wall is known: Dahl (1960) found that *Peloscolex benedeni* (Udekem) shed its cuticle and papillae at maturity, and Brinkhurst (1964) states that the freshwater *Peloscolex ferox* (Eisen) attains the papillate condition from a nonpapillate juvenile and then periodically, though not strictly seasonally, sheds its papillae. A study of 197 individuals of *L. verrucosus* in different states of maturity (Types and USNM 45292) has revealed the following variation pattern in its body wall: papillae are developed on segments IV or V to the terminal segment, prior to, or immediately after, emerging from the cocoon; the papillae grow with the animal and may also develop on the first few anterior segments; as the individual reaches sexual maturity there appears to be a progressive loss of papillae from the anterior end until the body wall is papillate only in the postclitellar region; after copulation and cocoon deposition, it appears that both the genitalia and the papillae regress, or the latter shed (as in *Peloscolex*).

The general body form and dimensions, the papillate body wall, and the number and form of the setae of *L. verrucosus* are strikingly similar to those of *Peloscolex gabriellae* Marcus, 1950. The latter appears to be a widespread, amphiamerican, marine species, or species complex, with very wide ecological tolerances (Cook, 1970b), and because its setal pattern is unique within *Peloscolex*, its presence is sometimes diagnosed on the basis of immature individuals. However, unless the gut diverticulum character, which is rarely checked in routine tubificid identifications, is examined, immature *P. gabriellae* and *L. verrucosus* can be mistaken for each other.

Limnodriloides barnardi, new species

Figure 5

Holotype.—USNM 48730. Bahia de San Quintin, station SQ 16. Depth, less than 2 m, in dark grey sandy silt. Collected 23 April 1960.

Paratypes.—USNM 48731. Two individuals, data as for holotype. Two individuals from SQ 8 (in black silt; collected 22 April 1960). One individual from each of SQ 19, 22, 30, 37, 46, 51, 85, 91; two individuals from SQ 15. NMC 3480. One individual from SQ 2. All paratypes collected April 1960 at a depth of less than 2 m.

Additional (non-type) material.—USNM 45291 and 45297.

Etymology.—Named for J. Laurens Barnard (Smithsonian Institution) who led the expedition to Bahia de San Quintin.

Description.—About 35 segments. 8 to 10 mm long. 0.12 to 0.20 mm in diameter anteriorly, 0.25 to 0.30 mm at clitellum, 0.10 to 0.16 mm posteriorly. Prostomium a little shorter than it is wide at the peristomium junction, with a small papilla anteriorly. Clitellum weakly developed on segments XI and XII. Dorsal and ventral setae similar in number, size and shape: somatic setae bifid, 40 to 60 μ long, with subequal teeth; in preclitellar region each setal bundle contains 3, sometimes two or four setae; posteriorly each bundle contains two setae. Each ventral bundle of segment X contains one slender, straight or curved, elongate spermathecal seta 110 to 120 μ long, which has a hollow groove from the node to the distal end; proximal end of spermathecal setae, on which the setal protractor muscles are inserted, are strongly hooked; distal half of spermathecal setae each enclosed in a pear-shaped sac, 65 to 70 μ long, 40 to 48 μ diameter, which consists of an inner layer of vacuolated cells and an outer muscle layer, and which connects with the body wall musculature. Ventral setae absent on segment XI. Paired male pores open in the line of the ventral setae on segment XI. Paired spermathecal pores open in the line of, or slightly lateral to the spermathecal setae (out of a total of 25 individuals examined for the character, 18 had spermathecal pores located anterior to the spermathecal setae, five had pores posterior to the setae, and two were without spermathecal setae).

Pharyngeal glands present in segments IV and V. Chloragogen cells begin in segment VI. Male genital system (all structures paired): conical male funnel situated ventrally on septum X/XI drains into the vas deferens, 9 to 12 μ diameter, about 180 μ long, which joins the atrium apically; atrium, whose long axis is directed anteriorly, consists of an ovoid to elongate ampulla, 100 to 110 μ long, 35 to 60 μ diameter, and an elongate duct, 95 to 135 μ long, 25 to 35 μ diameter, which terminates as the penis; a large, thickly-stalked prostate gland joins the atrial ampulla ventrally. Atrial ampulla consists of a thin outer muscle layer and an inner layer of thin lining cells. About the first 90 to 100 μ of the atrial duct (adjacent to the ampulla) is lined with thick, highly glandular cells. The penial complex consists of a more or less circular infolding of the body wall (the penial sac) 60 to 70 μ deep, 45 to 50 μ maximum

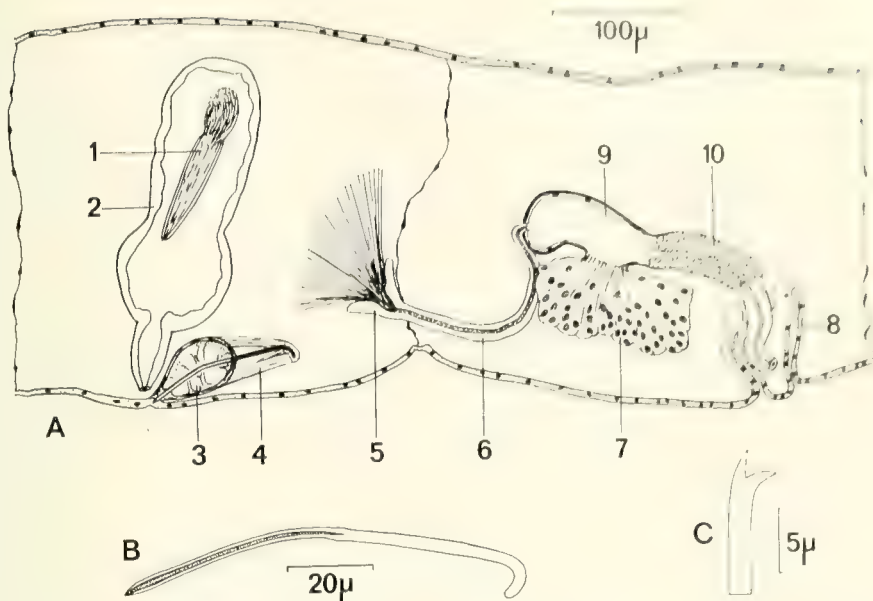


Figure 5. *Limnodriloides barnardi*, n. sp. A, Longitudinal view of genital segments; B, Spermathecal seta; C, Somatic seta. 1, sperm bundle; 2, spermathecal ampulla; 3, vacuolated muscular sac surrounding spermathecal seta; 4, protractor muscles of spermathecal seta; 5, male funnel; 6, vas deferens; 7, prostate gland; 8, penial sac; 9, atrial ampulla; 10, glandular part of atrial duct.

diameter, and a truncated-cone-shaped penis, through which penetrates the terminal part of the atrial duct; the latter opens on the penis subterminally and laterally. Paired spermathecae with discrete ducts 40 to 55 μ long, 30 to 35 μ maximum diameter, and elongate ampullae 200 to 220 μ long, 70 to 120 μ maximum diameter; latter tend to be constricted in the middle third of their length. Sperm in the spermathecae oriented into long narrow bundles, 95 to 135 μ long.

Remarks.—Morphologically, *L. barnardi* is very closely related to *L. winckelmanni*. Their atria and atrial ducts with glandular lining cells are, on available evidence, indistinguishable, and their spermathecal setae contained within vacuolated sacs are unique in the genus; the number and form of their setae are also similar. A comparison of the information available on *L. winckelmanni*, which is apparently derived from the type specimens alone (Michaelsen, 1914; Boldt, 1928; Hrabě, 1967; 1971b) with the description of *L. barnardi*, reveals that their intromittent organs differ (*vide infra*) and that the general dimensions of *L. barnardi* are smaller than those of *L. winckelmanni* (maximum body length, clitellum diameter and setal length of the two species are, respectively, 10 and 18 mm, 0.3 and 0.6 mm, 60

and 90 μ). The dimensions are probably not important characters as wide intra-specific variation in size is well known for many common tubificids and lumbriculids, but the different structures of their intromittent organs is more fundamental. Hrabě (1971b) showed that in *L. winckelmanni* small pseudopenial papillae cover the simple openings of the male ducts from the side. In *L. barnardi*, however, a large penial sac contains the terminal end of each atrial duct which opens subterminally on a truncated cone-shaped penis; employing present definitions of the terms, it would appear that the proximal part of this organ can be termed a true penis while the part distal to the actual male orifice could be considered as a pseudopenis.

ECOLOGICAL COMMENTS

The eastern arm of Bahia de San Quintin (referred to hereafter merely as "the bay") is a shallow body of water of more or less uniform salinity. At high tide the water depth over about 85 percent of the bay is less than two m: narrow, steep-sided channels (six to eight m deep) account for the remaining 15 percent (Barnard,

TABLE 1. Station data and number of tubificids in each bay sample. A—station number; B—fraction of sample counted and identified (S indicates subsamples of 30 worms); C—total number of tubificids, including immature specimens (numbers in brackets are estimated); D—mean particle diameter in μ ; 1—*Tubifex postcapillatus*; 2—*Thalassodrilus belli*; 3—*L. monotheucus*; 4—*L. verrucosus*; 5—*L. barnardi*.

A.	B.	C.	D.	1.	2.	3.	4.	5.
1	S	(130)	7	4	7	—	13	3
2	all	12	6	—	8	—	2	1
3	all	9	7	—	4	—	—	2
4	all	1	7	1	—	—	—	—
5	S	(300)	6	3	1	—	12	5
6	S	(75)	9	—	2	—	13	—
7	all	44	30	—	3	—	12	10
8	S	(200)	13	—	—	5	—	13
9	S	(100)	16	4	2	1	4	5
10	S	(200)	38	—	—	2	—	22
11	S	(150)	21	—	—	3	—	17
12	all	23	98	—	1	—	—	8
13	10%	4	26	—	—	—	—	2
14	S	(250)	56	—	—	3	2	17
15	20%	33	71	—	—	1	—	16
16	all	34	32	—	—	8	1	16
17	S	(150)	22	—	—	2	—	21
18	all	11	61	—	—	1	—	1
19	S	(300)	49	—	—	5	3	16
20	all	26	105	—	—	3	4	11
22	all	1	174	—	—	—	—	1
23	S	(400)	36	—	—	5	—	23
24	all	7	13	—	—	—	1	1
25	all	2	143	—	—	—	—	1
26	S	(300)	19	11	—	—	5	2
30	10%	6	19	—	—	—	—	4
31	10%	21	52	—	—	—	—	4
32	all	16	33	—	—	1	—	3
35	all	47	58	—	—	3	18	16
36	S	(80)	51	—	—	5	—	21
37	S	(250)	31	—	—	3	6	9
38	all	58	43	—	—	1	26	21
39	S and 15%	(100)	54	—	—	—	23	7
40	all	3	242	—	—	1	—	1
41	S	(150)	33	—	—	5	11	11
42	S	(100)	?	—	—	—	17	5
43	S	(500)	53	13	—	—	1	11
45	all	6	36	—	—	—	1	2
46	all	11	51	—	—	—	10	1
47	S	(275)	79	—	—	6	—	21
49	S	(225)	?	—	—	—	28	—
50	all	37	?	—	—	—	37	—
51	S	(75)	63	—	—	2	4	16
53	all	1	78	—	—	—	—	1
54	S	(175)	?	—	—	—	25	5
58	all	30	46	—	—	—	23	7
60	S	(75)	54	—	—	—	28	2
64	S	(250)	48	—	—	—	14	13
74	all	4	103	—	—	—	—	4
75	all	4	142	—	—	—	1	3
76	S	(75)	66	—	—	9	2	17
79	all	1	55	—	—	—	1	—
85	all	11	88	—	—	—	—	8
88	all	18	137	—	—	—	1	15
91	all	46	98	—	—	—	—	23

1962) and at low tide much of the bay floor is exposed or only sparsely covered by shallow pools. The depth and salinity of the water, *per se*, are not considered to be significant factors in controlling the distribution of the Tubificidae in this study although the amount of exposure of the habitat at low tide, the degree of evaporation, and the water retention characteristics of the sediment, probably are. Such data are not available, but related sediment parameters, the mean particle size and sorting coefficient, are known for most of the bay stations. A textural analysis of the bottom sediments demonstrated that a continuous range of conditions exist in the bay, from coarse, well-sorted sands, to poorly-sorted clays which dominate the north end of the bay; a complex mosaic of intermediate sediment types occur in the central regions, and sands predominate in the bay's south end (Gorsline and Stewart, 1962). The latter authors also showed that, in general, the organic content of the sediment increased with decreasing particle size, hence it is probable that the amount of food available to oligochaetes is inversely proportional to this parameter. Therefore, the mean particle size of the sediment is thought to be a direct or indirect measurement of some factors determining tubificid distributions in this study, and will be considered in more detail below.

The numbers of each tubificid species identified from each San Quintin station (each sample = 0.065 m²) and other relevant data are summarized in Table 1; for purposes of brevity, and to facilitate comparisons with other studies, mean sediment particle sizes are discussed in terms of ϕ units ($\phi = \log_2$ particle diameter in mm, hence diameters of $4 - 8 \mu = 8 \phi$, $8 - 16 \mu = 7 \phi$, $16 - 31 \mu = 6 \phi$, $31 - 62 \mu = 5 \phi$, $62 - 125 \mu = 4 \phi$, $125 - 250 \mu = 3 \phi$). From this information, and the locations of the benthic stations (Fig. 6) the distribution and density of each species can be inferred.

Abstracting and comparing pertinent data from table 1, it is evident that the three species of *Limnodriloides* bear a definite relationship to very fine sand and silt (4 to 6ϕ optimum) in terms of both their frequency of occurrence and population size. The dominant tubificid, *L. barnardi*, occurred at 48 stations comprising all sediment classes, but was most frequently found in 4 and 5ϕ sediments (21 percent and 40 percent of its stations respectively); maximum population density of *L. barnardi* occurred in the 4 to 6ϕ range. *L. monothecus* occurred at 21 stations

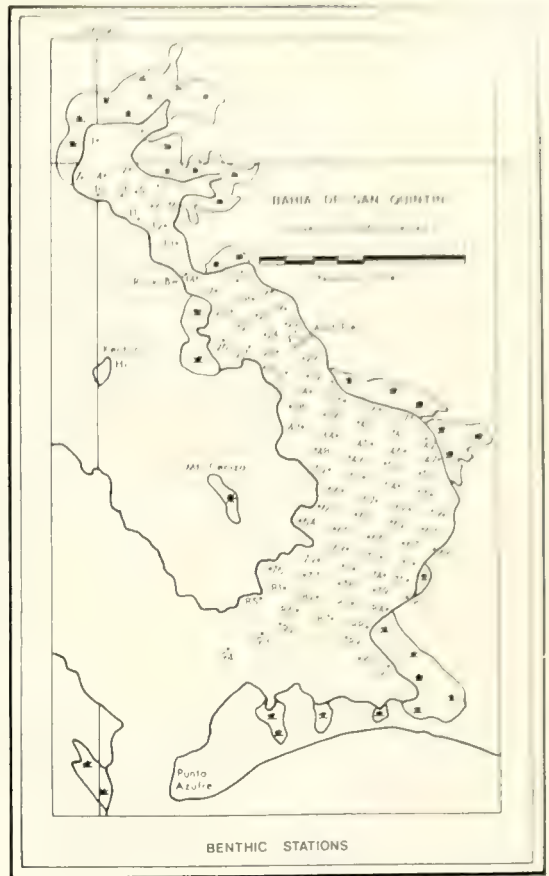


Figure 6. Locations of benthic sampling stations in Bahia de San Quintin; redrawn from Barnard, 1962.

of which 52 percent had 5ϕ sediments and 24 percent were 4ϕ . However, the population density of this species was remarkably constant over its whole sediment range of 4 to 7ϕ (about 280/m²). Of the 28 stations occupied by *L. verrucosus*, half had sediments in the 5ϕ class, with the remainder distributed fairly evenly over the whole sediment range of 3 to 8ϕ ; however, the abundance of *L. verrucosus* was highest in 5 to 6ϕ and 8ϕ substrates which may indicate that while it is capable of exploiting the finest sediments, it is partially excluded from them in this situation by competition with other deposit feeders or by the effects of predation.

The two remaining tubificids, *Tubifex pacificus* and *Thalassodrilus belli*, appear to be associated with the finest sediments which are located mainly at the north end of the bay. *Tubifex belli* was present in only eight samples but half of these were in the 8ϕ class in which

the maximum abundance for this species (460 m^{-2}) was also recorded. Only six stations were occupied by *T. postcapillatus* but three of these had 8 ϕ sediments. However, the species was strikingly more abundant in the 5 and 6 ϕ classes (about 3300 and 1700 worms/ m^2 respectively, compared with about 250/ m^2 in 8 ϕ sediments); except for the 8 ϕ class, these density figures were calculated from single samples whose numbers were, in turn, derived from subsamples, therefore large errors in them are possible. If the figures do reflect real trends, however, it is possible that *T. postcapillatus* has a wide sediment tolerance but is competitively restricted by *T. belli* or other detritivores in fine substrates (hence its low densities) and by *Limnodriloides* species in intermediate sediments; the latter is supported by the fact that at the 5 and 6 ϕ sediment stations where *T. postcapillatus* was abundant, *L. monothecus* was absent while *L. verrucosus* and *L. barnardi* were at relatively low densities.

DISCUSSION

That the distribution of freely burrowing benthic animals which feed upon their surrounding medium should be determined, in part at least, by sediment characteristics, is hardly surprising; at the extremes, a well-sorted, coarse-sand environment could be compared to rocky ground, while fine silts and clays are comparable with a rich and fertile loam. In Bahia de San Quintin, available habitats are restricted to the productive end of the scale and hence discrete communities of oligochaetes, such as those demonstrated in Cape Cod Bay, Massachusetts (Cook, 1971) cannot be delineated. However, even in the comparatively restricted sediment range of the bay, it is possible to recognize that 1) the finest silts and clay-silt are usually inhabited by *T. postcapillatus* and *T. belli* and 2) intermediate silts and fine-sands are usually exploited by *L. barnardi*, *L. monothecus*, and *L. verrucosus*. Although complicated by the differing availability of organic matter in the different substrate types, these trends support the conclusions of Bülow (1957), Brinkhurst and Kennedy (1962), Lasserre (1967), and Cook (1971) who all demonstrated that zones of differing sediments support different oligochaete faunas in the marine environment; similarly Reish (1963) found that many polychaetes in Bahia de San Quintin were associated with definite sediment types.

West coast marine oligochaetes are very poorly

known; the studies by Brinkhurst and Simmons (1968) reporting on the oligochaetes, mainly Tubificidae, of the San Francisco Bay system, Tynen's (1969) description of some littoral Enchytraeidae from Vancouver Island, and the present paper, summarize existing knowledge of the class in the northeastern Pacific. Brinkhurst and Simmons (1968) found *Peloscolex gabriellae* to be the dominant oligochaete in San Pablo Bay, and south San Francisco Bay where *Peloscolex apectinatus* and *Peloscolex nerthoides* also occurred in significant numbers; these authors did not relate substrate particle size with species distributions as it was felt that the study area was uniformly available to the constituent species and that other, chemical or biological, determining factors dominated. This is undoubtedly true in some situations, and especially so in the case of polluted waters (as in San Francisco Bay). As well as increasing nutrient concentrations, many sources of organic pollution can be expected to modify bottom deposits in the direction of lowering mean particle size and hence to decrease the diversity of niches available to free-burrowing benthic organisms. Thus these results, and those of authors who report definite correlations between sediment and species distributions, are not necessarily contradictory. For example, organic enrichment or increased siltation of Bahia de San Quintin could be expected to eliminate some of the tubificids described in this paper, and from the data presented here it is possible that *L. barnardi* and *L. monothecus* could be the sensitive species; the modified distribution of the remaining three species of Tubificidae may, under these circumstances, be very difficult to relate to any sediment parameter.

Indeed these speculations lead to the conclusion that failure to detect a clear relationship between species distributions and physical sedimentary parameters may, if a diversity of sediment types are known to exist, indicate environmental deterioration.

A growing preoccupation of aquatic biologists is the concern to detect, assess and monitor sources of environmental contamination and approaches have varied from a search for indicator species to sophisticated treatments of whole systems. The success of any biological investigation, however, depends basically on accurate taxonomy; the point is stressed because this study has demonstrated that confusion between the two marine tubificids *Limnodriloides verrucosus* and *Peloscolex gabriellae* could arise if identifications

are based on superficial characteristics (papillation and setal pattern). The importance of this distinction further lies in the fact that *P. gabriellae* is resistant to high levels of organic pollution while the tolerance characteristics of *L. verrucosus* are unknown.

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A NEW SPECIES OF FOSSIL *NUTTALLIA* (MOLLUSCA: BIVALVIA) FROM THE PLIOCENE OF SONOMA COUNTY, CALIFORNIA

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ABSTRACT: *Nuttallia jamesi*, new species, is described from strata assigned Pliocene age in the Sebastopol quadrangle, central Sonoma County, California. The species is similar to *N. nuttallii* (Conrad), late Miocene to Recent of California and Baja California, and to *N. olivacea* (Jay), Miocene to Recent of Japan, but differs from both in having an acuminate posterior end. The genus *Nuttallia* is restricted, in both Recent and fossil occurrence, to the north Pacific basin. It represents a temperately adapted branch of the predominantly tropical Sanguinolariinae.

Several years of field work by one of us (Guruswami-Naidu) at an exposure of soft sandstone in central Sonoma County, California, mapped as Merced Formation by Travis (1952), have resulted in a collection of more than forty marine invertebrate species (mostly mollusks) and numerous bird, fish, and mammal remains. Among the mollusks represented is a new species of the tellinacean bivalve genus *Nuttallia*, described herein. An account of the associated fauna and paleoecology will appear in a report now in preparation.

FAMILY PSAMMOBIIDAE FLEMING, 1828
SUBFAMILY SANGUINOLARIINAE GRANT AND GALE,
1931

Genus *Nuttallia* Dall, 1898

Nuttallia Dall, 1898: 58 [proposed as "section" of *Sanguinolaria* Lamarck, 1799]; Dall, 1900; Coan, 1973.

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Type species, by original designation, *Sanguinolaria nuttallii* Conrad, 1837; late Miocene to Recent, California and Baja California.

Dall (1900) characterized *Nuttallia* as follows: "Shell large, suborbicular, inequivalve, more or less twisted, the right valve slightly flatter, the posterior cardinal in the left valve obsolete; the pallial sinus narrower in front and somewhat detached from the pallial line." He gave this contrasting description of *Sanguinolaria, sensu stricto*: "Shell moderately large, thin, equivalve, short, rose-colored or white, with short, inconspicuous nymphs, two bifid cardinal teeth in each valve; pallial sinus deep, widest in front, confluent with the pallial line below, the epidermis thin, dehiscent" (Dall, 1900). Living species of *Nuttallia* have a persistent, dark, generally glossy periostracum and a strong cardinal ligament borne on a projecting nymph. Fossil specimens with valves paired are relatively common. Coan's (1973) review of Recent northwest American Psammobiidae included a discussion of *Nuttallia nuttallii* (Conrad, 1837), type species of the genus and the only species known to be living in eastern Pacific waters. Kira (1953) reviewed the Recent Japanese species; Habe and Ito (1965) provide a later summary and synonymy.

Recent authors are almost evenly divided on whether to call *Nuttallia* a genus or a subgenus. It is often ranked as a subgenus of *Sanguinolaria* Lamarck, 1799 (type species, *Solen sanguinolentus* Gmelin, 1791), and occasionally as a subgenus of *Soletellina* Blainville, 1824 (type species, *Soletellina radiata* Blainville, = *Solen diphos* Linnaeus, 1771). (*Soletellina* is a junior synonym of *Hiatula* Modeer, 1793, since *Solen diphos* Linnaeus is the type species of the latter genus by subsequent designation [Stoliczka, 1870: 114]. A later designation [Winckworth, 1935] of *Mya truncata* Linnaeus, 1758, as type species of *Hiatula* is invalid.) As originally proposed by Grant and Gale (1931) the family Sanguinolariidae contained the genera *Gari* Schumacher, 1817, *Tagelus* Gray, 1847, and *Sanguinolaria* (including "section" *Nuttallia*), and was thus practically coextensive with Coan's (1973) usage of Psammobiidae Fleming, 1828. Keen (1969) reduced Sanguinolariidae to subfamily rank, including only the genus *Sanguinolaria* and under it seven subgenera, *Nuttallia* among them. In both morphology and distribution, *Nuttallia* seems sufficiently distinct from *Sanguinolaria* to receive generic rank, with its affinity expressed at the subfamilial level.

Typical *Sanguinolaria* species are tropical in

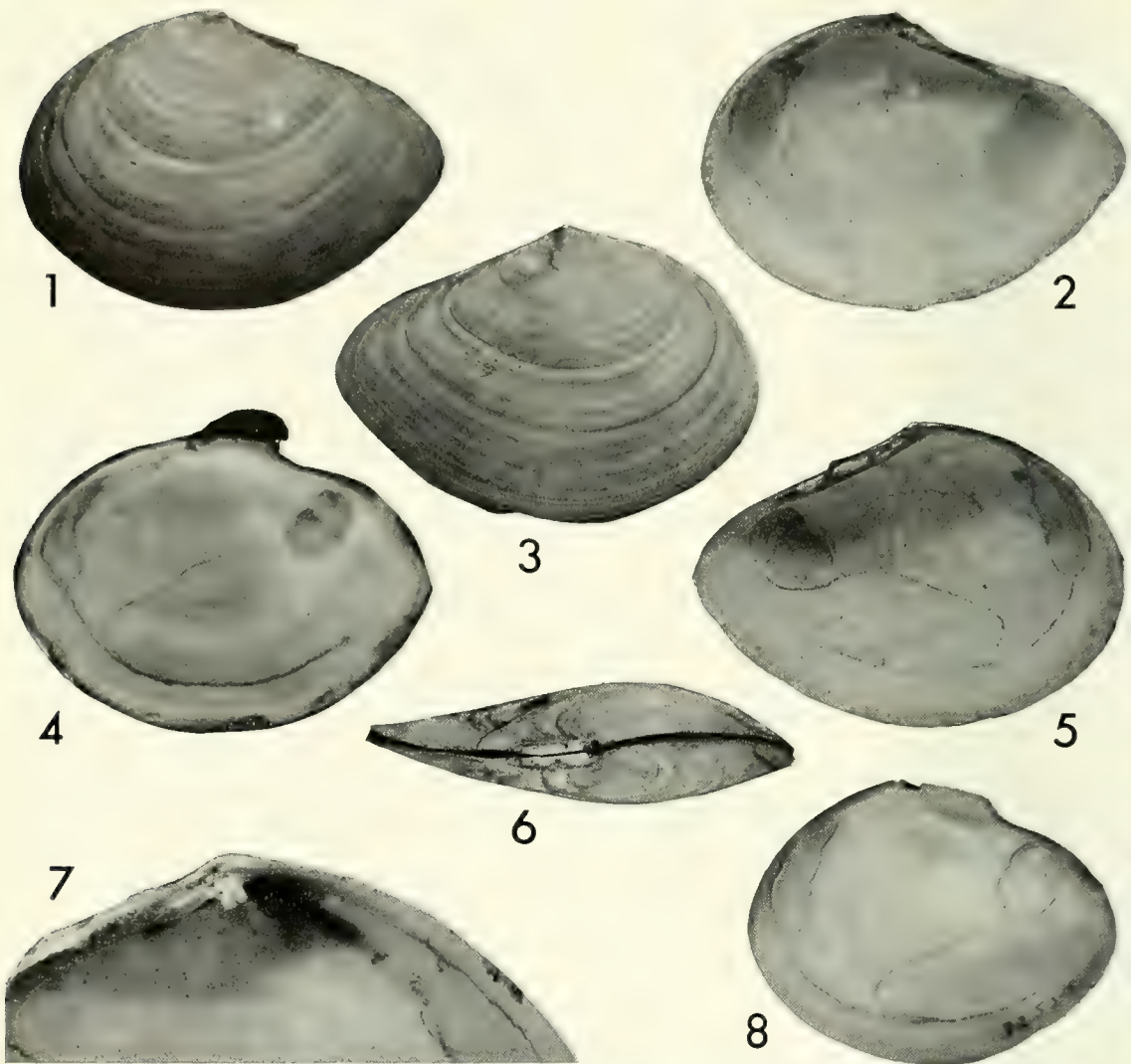
distribution and occur in the eastern Pacific, and Panamic (eastern Pacific). In the Panamic province, the northern limit for species of *Sanguinolaria, sensu stricto* is San Ignacio Lagoon, Baja California (Clark, 1971), approximately 26° 45' north latitude, the 19° C February surface isotherm (Durham, 1950: fig. 2). Species of *Nuttallia* now occur in warm-temperate to cool waters in the north Pacific Ocean, and fossil occurrences are restricted to the margins of the north Pacific basin. Recent *N. nuttallii* ranges from Bodega Bay, California (38° 20' N), to Magdalena Bay, Baja California (24° 40' N) (Coan, 1973). Its range includes the southern portion of the Oregonian molluscan province, all of the Californian province, and the northern part of the Surian province, in the definitions of Valentine (1966). Valentine's Surian province is essentially equivalent to the portion of the west coast of Baja California regarded by Addicott (1966) as an area of provincial overlap, with Californian forms predominating in outer-coast biotopes and Panamic forms dominant in protected biotopes. By neither criterion is *Nuttallia nuttallii* a truly Panamic species, as one might infer from Coan's (1973: table 3) distributional tabulation. Kuroda and Habe (1952) cite the western Pacific species *Nuttallia petri* (Bartsch, 1929) as ranging from 43°–46° N, *Nuttallia olivacea* (Jay, 1857) from 30°–43° N, and *Nuttallia "nuttallii" (?)* [= *N. ezonis* Kuroda and Habe in Habe, 1955] from 39°–51° N. Both the western and eastern Pacific species which range into warm water—*N. nuttallii* and *N. olivacea*—are also found considerably farther north, in cool-temperate marine climates.

Phyletic separation of *Nuttallia* from *Sanguinolaria* dates from the Paleocene. The oldest known *Nuttallia*, *N. townsendensis* (Clark, 1925) from the late Eocene Quimper sandstone of Washington, occurs in a fauna of distinctly tropical aspect (Durham, 1950). The similar *N. uchigoensis* Kamada, 1962, from the upper Oligocene or lower Miocene Asagai Formation of Honshu, occurs in a molluscan assemblage suggestive of warm-temperate conditions and deposition offshore in moderate depths. Later Tertiary species show increasing adaptation to cooler conditions.

Nuttallia jamesi, new species

Figures 1–3, 5–7

Diagnosis: A small, thin-shelled species of *Nuttallia* with acuminate posterior end, narrow pallial sinus,



Figures 1–3, 5. *Nuttallia jamesi*, new species; external and internal views of holotype (CAS Department of Geology No. 54330). Length 53.4 mm. Figure 4. *Nuttallia nuttallii* (Conrad); internal view of right valve with ligament attached; Recent, southern California (CAS Department of Geology No. 54335). Length 62.2 mm. Figure 6. *Nuttallia jamesi*, new species; dorsal view of paratype (CAS Department of Geology No. 54331). Length 46.8 mm. Figure 7. *Nuttallia jamesi*, new species; detail of hinge of left valve of paratype (CAS Department of Geology No. 54332), nymph partly broken. Figure 8. *Nuttallia olivacea* (Jay); internal view of right valve; Recent, Iwai Mura, Chiba Prefecture, Japan (CAS Department of Geology No. 54334). Length 54.0 mm.

and hinge line sinuous in dorsal view, curving to the left posteriorly, to the right anteriorly.

Description: Shell small for the genus, thin; inequivalve, left valve more inflated than right valve; beaks situated at midline; anterior end of shell broad, evenly rounded, posterior end acuminate; surface of valves smooth except for incremental lines of varying strength. Hinge line shallowly sinuous in dorsal view, curving to the left posteriorly, to the right anteriorly.

Right valve most inflated at about $\frac{1}{3}$ of distance from beak to anterior end; compressed along both dorsal margins and along postero-ventral margin; with a radial angulation slightly below posterior dorsal margin; beak small, pointed; hinge plate narrow, with two diverging, oblique cardinal teeth, the posterior tooth larger and bifid; anterior dorsal margin convex; posterior dorsal margin concave, with a narrow escutcheon proximally, in which rises an elongate,

broad-topped nymph; pallial sinus narrow, deep, extending about $\frac{1}{3}$ of the distance anterior to midline, recurring before joining pallial line at an acute angle; muscle scars large; internal margin smooth. Left valve most inflated directly below beak; slightly compressed along posterior dorsal margin; with a blunt radial angulation running from beak to extreme posterior point of valve, and a shallow radial sulcus below this; beak elevated, small but prominent; hinge plate narrow, somewhat excavated, with a projecting, bifid anterior cardinal tooth (broken on holotype) and a small, nearly horizontal, laminar posterior cardinal tooth separated from the anterior tooth by a hollow; no lateral teeth present; posterior dorsal margin with a narrow escutcheon, in which rises a nymph, pairing with that of the right valve; pallial sinus and muscle scars like those of the right valve; internal margin smooth.

Dimensions: Holotype, length 53.4 mm; height 37.0 mm; diameter (both valves) 14.8 mm. Measured paratypes: (a) length 49.2 mm; height 36.6 mm; diameter 13.5 mm; (b) length 46.8 mm; height 33.9 mm; diameter 12.5 mm; (c) length 44.0 mm; height 32.9 mm; diameter 11.4 mm.

Type material: Holotype, right and left valves, No. 54330, Department of Geology, California Academy of Sciences. Paratypes, Nos. 54331–54333, same institution. Paratypes have been deposited in the following institutions: Department of Paleobiology, U. S. National Museum of Natural History; Museum of Paleontology, University of California, Berkeley; Department of Paleontology, Los Angeles County Museum of Natural History; Department of Geology, Stanford University; Institute of Geology and Paleontology, Tohoku University, Sendai, Japan.

Type locality: California Academy of Sciences Department of Geology locality No. 54164, roadcut in grayish-white, poorly indurated and highly fossiliferous sandstone on north side of River Road, 0.2 miles north of town of Trenton and 0.3 miles east of intersection of River Road and Trenton-Healdsburg Road, United States Geological Survey Sebastopol, California, quadrangle, 15 minute series (topographic), 1954 edition, Sonoma County, California (approximately 38° 29' N, 122° 51' W). On the geologic map of the Sebastopol quadrangle prepared by Travis (1952: pl. 1), the locality is at the fault contact between the Pliocene Merced Formation and "Jurassic" serpentine.

The species is named for Mr. James Nikas, student of west American paleontology, who first suggested that the taxon was undescribed.

DISCUSSION

Comparisons: The only *Nuttallia* previously recorded from Pliocene strata in western North America is *N. nuttallii* (Conrad, 1837). It has been reported in the Jacalitos, Etchegoin, and San Joaquin Formations on the west side of the San

Joaquin Valley (Nomland, 1917; Stewart and Richards, 1940 [1941]). Its most occurrence. Recent or fossil, is in the Pliocene Falor Formation (University of California Museum of Paleontology inverted locality A-4234) of the Blue Lake quadrangle, Humboldt County, California. These two specimens were reported by Manning and Ogle (1950) as *Sanguinolaria nuttallii*, and appear to be typical of the species. *Nuttallia nuttallii* has a geologic range of late Miocene (Neroly) (Weaver, 1949) to Recent.

Nuttallia nuttallii (Fig. 4) is more inequivalve than *N. jamesi*, with the right valve nearly flat and the left valve strongly convex. The posterior end of *N. jamesi* is acutely pointed; that of *N. nuttallii* is broad, ending in an obtuse posterior angle. In dorsal view, the hinge line of *N. nuttallii* is less conspicuously sinuous than that of *N. jamesi*. The beaks of *Nuttallia nuttallii* are more anterior and the cardinal nymph is proportionally shorter and higher than on like-sized specimens of *N. jamesi*. The nymph of large specimens of *N. nuttallii* is low and elongate. In contrast to the relatively narrow pallial sinus of *N. jamesi*, the sinus of *N. nuttallii* is broad and trapezoidal and, although variable, is generally deeper, extending about half the distance anterior to the midline. The material at hand indicates that *N. jamesi* is a smaller species than *N. nuttallii*, which commonly reaches 90 mm and may reach 150 mm in length.

The nominal form *Sanguinolaria orcutti* Dall, 1921, described from the Pleistocene of San Quintin Bay, Baja California, and considered by Grant and Gale (1931) and Coan (1973) to be synonymous with *N. nuttallii*, is also larger than *N. jamesi*, with a broad, obtuse posterior end and trapezoidal pallial sinus. *Nuttallia toulai* (Hertlein and Jordan, 1927) from the Miocene of Baja California, is another large, suborbicular form, without the acuminate posterior end of *Nuttallia jamesi*.

Nuttallia olivacea (Jay, 1857) (Fig. 8), a common Recent species in Japan, also recorded as early as the Miocene, is in some respects the species most similar to *N. jamesi*. Both species are of similar size, with pallial sinuses of the same general shape. *Nuttallia olivacea*, however, has a bluntly angular posterior end, hinge line straight in dorsal view, a solid hinge plate, and both dorsal margins convex, while *N. jamesi* has a sharp posterior angle, hinge line sinuous in dorsal view, narrow hinge plate, and a concave posterior dorsal margin.

Other Asian Pliocene and Quaternary species are less similar. *Nuttallia ezonis* Kuroda and Habe in Habe, 1955, is morphologically very close to *N. nuttallii*, under which name it was reported by earlier workers. The record of "*Sanguinolaria (Nuttallia) nuttallii*" from upper Pliocene strata on the western coast of Kamchatka (Slodkewitsch, 1938) is probably referable to *N. ezonis*. *Nuttallia commoda* (Yokoyama, 1925), described from the Pliocene of Japan, is a large, subquadrate, equivalve species with concentric ridges crossing the shell. The Recent northwestern Pacific *Nuttallia petri* (Bartsch, 1929) is regarded by Habe and Ito (1965) as a synonym of *N. commoda*. *Nuttallia ochotica* (Slodkewitsch, 1936), an upper Pliocene species from the western coast of Kamchatka, also has low concentric ridges and, if not identical with *N. commoda*, is probably closely related to it.

Age: Travis (1952) considered the Merced Formation in the Sebastopol Quadrangle to be "probably upper Pliocene in age," based on both faunal criteria and local superposition with the middle to upper Pliocene Petaluma Formation. This age assignment of the Petaluma formation is based on remains of the horse, *Neohipparion gidleyi* Merriam, 1915, a species of Hemphillian age (Stirton, 1952). Berggren's (1971: table 52:40) Cenozoic radiometric time-scale places the Hemphillian stage in the interval 3.5–10 million years before present, late Miocene to mid-Pliocene in terms of the European series-epoch classification.

Fossils from Wilson Grove, 2 miles north of Trenton, were regarded by Dickerson (1922) as equivalent to the fauna of the type Merced Formation on the northern San Francisco Peninsula. Recent field work has shown several distinct faunal assemblages, indicating different environmental and depositional conditions, within the Sonoma County Merced Formation. The stratigraphic relationships of these and other published localities to the type locality of *Nuttallia jamesi* are obscured by lack of exposures and local faulting. A radiometric age of six million years has been obtained from tuff interbedded in Merced Formation sandstones in the Sebastopol quadrangle (G. H. Curtis, personal communication). We have not determined the stratigraphic relationship of this tuff to the type locality of *N. jamesi*.

Approximately one-third of the molluscan taxa at CAS locality 54164 are extinct. *Protothaca staley* (Gabb, 1866), *Nucella trancosana* (Arnold, 1908), *Nassarius (Caesia) grammatus* (Dall,

1917), *Nassarius (Demondia) californianus* (Conrad, 1856), *Ophiodermella graciosa* (Arnold, 1907), and *Megasurcula remondii* (Gabb, 1866) are among the extinct species widespread in strata traditionally classified as Pliocene in the west American provincial sequence. The presence of *Nassarius (Caesia) grammatus* and the absence of *N. (C.) moranianus* (Martin, 1914) would seem to exclude an uppermost Pliocene or early Pleistocene age for this fauna (cf. Addicott, 1965: B6–B8, fig. 1). This line of evidence places CAS locality 54164 stratigraphically below all or part of the Merced section at Bolinas, Marin County, California, the type locality of *Nassarius moranianus*. The presence in the fauna of an undescribed echinoid of the genus *Scutellaster* may afford more precise placement within the west coast faunal sequence (J. W. Durham, pers. comm.). We conclude that the assemblage is Pliocene in the traditional terminology of west coast paleontologists, but possibly should be called late Miocene in reference to the European series-epoch classification.

Paleoecology: The molluscan assemblage at the Trenton locality suggests deposition on a silty sand bottom in 15 to 40 meters depth, with several elements transported downslope from rocky and sandy intertidal and shallow subtidal areas probably less than a mile distant. As will be discussed in a forthcoming paper, several features of the fauna support analogy with present-day conditions at the southern end of Monterey Bay, California. Paired, intact valves (seven pairs in the type lot) of the rather thin-shelled *Nuttallia jamesi* might be interpreted as suggesting burial in place, rather than transport into the assemblage. Much of the fossil material from locality 54164, however, consists of indeterminable pelecypod fragments; thus the type lot represents an unknown fraction of the total *Nuttallia* component of the faunule.

Recent *Nuttallia nuttallii* usually lives intertidally in protected bays, particularly in entrance channels washed by fast-moving tides, buried in loose sand or mixed sand and gravel (Fitch, 1953). It is less common on the open coast, where it occurs in sand below wave-base. The greatest depth from which the species is reported is 10 meters (Coan, 1973). The Japanese species, *Nuttallia olivacea*, has been reported from sandy and muddy bottoms, intertidally to 10 m (Kuroda, Habe, and Oyama, 1971). *Nuttallia ezonis* was cited by Habe (1964) as occurring on fine sand

bottoms from low tide level to "several" meters depth.

ACKNOWLEDGMENTS

The authors are indebted to J. Wyatt Durham, Peter U. Rodda, and Eugene V. Coan for advice on various aspects of this study. Warren O. Addicott loaned specimens for comparison. A. Myra Keen advised us concerning a nomenclatural detail. G. H. Curtis kindly allowed citation of a radiometric date. The professional assistance of Clara Gross, Assistant Librarian, California Academy of Sciences, is especially appreciated.

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TWO NEW SPECIES OF LAND SNAILS FROM THE PINALENO MOUNTAINS, ARIZONA

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ABSTRACT: Two new species of land snails are described from the Pinaleno Mountains in southeastern Arizona.

The Pinaleno Mountains, sometimes called the Graham Mountains, lie in line with the Chiricahua system in southeastern Arizona and are separated from the northern end of the Dos Cabezas Mountains by a wide mesa. The Pinalenos have long been neglected by malacologists. A brief account is given (Pilsbry and Ferriss, Proc. Acad. Nat. Sci. Philadelphia, for 1918: 282-334, 1919) of a collecting trip made by Ferriss, 14 October 1913, "Besides *Sonorella* and *Oreohelix*, *Vitrina alaskana* was abundant and two young Vallonias were found." Pilsbry and Ferriss described *Sonorella grahamensis* from this material but there was no further mention of the *Oreohelix*.

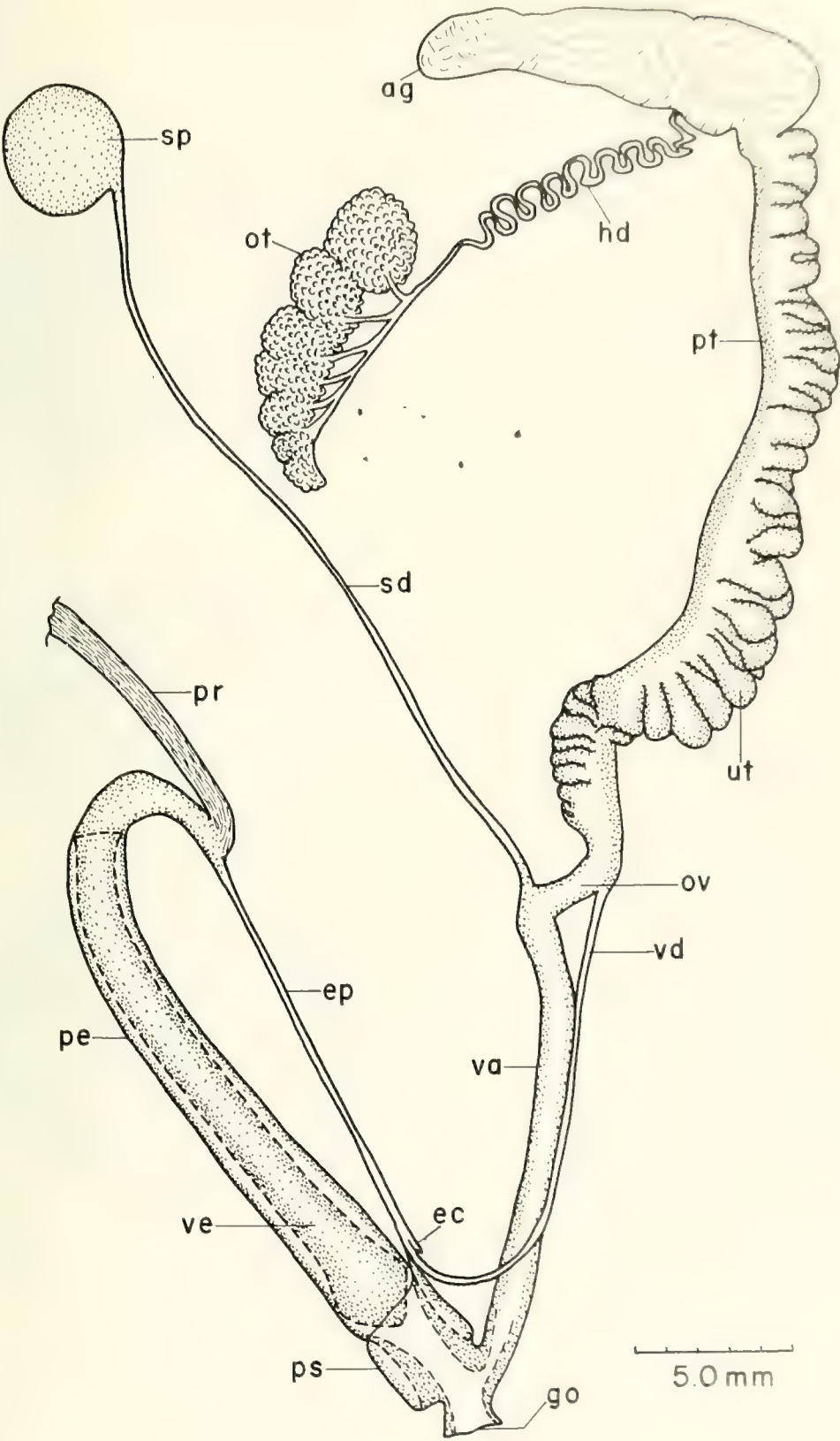
On 21 April 1954, M. L. Walton and one of us (Gregg) visited the Pinaleno Mountains.

Leaving Safford on US highway 666, we traveled south seven miles, then turned west on the "Swift Trail," now a well-maintained mountain road. We continued about 20 miles which took us to near 9000 feet altitude. Stopping now and then to look for snails, we found *Sonorella* and *Oreohelix* and in the same microhabitat, *Microphysula ingersolli meridionalis* (Pilsbry and Ferriss), *Retinella indentata paucilirata* (Morelet), *Zonitoides arboreus* (Say), *Striatura meridionalis* (Pilsbry and Ferriss), *Deroceras* sp., *Discus*

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Figure 1. *Sonorella imitator*, new species. Genitalia drawing made from projection of stained whole mount: ag, albumin gland; ec, epiphallallic caecum; ep, epiphallus; go, genital orifice; hd, hermaphroditic duct; ot, ovotestes; ov, oviduct; pe, penis; pr, penial retractor; ps, penial sheath; pt, prostate; sd, spermathecal duct; sp, spermatheca; ta, talon; ut, uterus; va, vagina; vd, vas deferens; ve, verge.



cronkhitei (Newcomb), *Punctum californicum* Pilsbry, and *Vertigo gouldi arizonensis* Pilsbry. These snails were found under isolated rocks; no definite rockslides were present. The *Oreohelix* from this locality immediately appeared to be different from any described species. The *Sonorella* specimens appeared to be *S. grahamensis* Pilsbry and Ferriss but subsequent dissection revealed two distinct species, *S. grahamensis* and an undescribed species, both sympatric in the same microhabitat. The new *Oreohelix* and the new *Sonorella* are described below. All measurements are given in millimeters.

FAMILY HELMINTHOGLYPTIDAE

Sonorella imitator, new species

Figures 1 and 2

This name was cited as a nomen nudum by Bequaert and Miller, The Mollusks of the Arid Southwest, p. 117, 1973.

Diagnosis.—A species of moderate size, finely striate body whorl, characterized anatomically by a very long verge and a short oviduct.

Description of Holotype.—Shell heliciform, depressed conic, whorls four and one half, increasing gradually to the last whorl which is moderately expanded and descends behind the aperture so that the last one eighth of the body whorl lies at an angle of about 25 degrees with the transverse axis of the shell. Whorls convex, flattened above, rounded on the base. Aperture rounded-oval and lying at an angle of about 45 degrees with the vertical axis. Peristome very slightly expanded, not appreciably thickened, and with a thin parietal callus; the columellar end of the peristome slightly reflected over the margin of the umbilicus. Width of the umbilicus contained about seven times in the greater diameter of the shell. Surface glossy, color light sayal brown, lighter on the base and on each side of the peripheral chestnut brown band. Embryonic shell consists of one and one half whorl, apex smooth, followed by indistinct radial wrinkling which continues over the remainder of the embryonic portion of the shell and as far as the first half of the penultimate whorl where it is replaced by delicate growth lines. Early whorls have a minutely granulose appearance with here and there suggestions of papillae which have been nearly effaced by erosion. There are numerous impressed spiral lines on the upper surface of the body whorl and on the last half of the base of the body whorl.

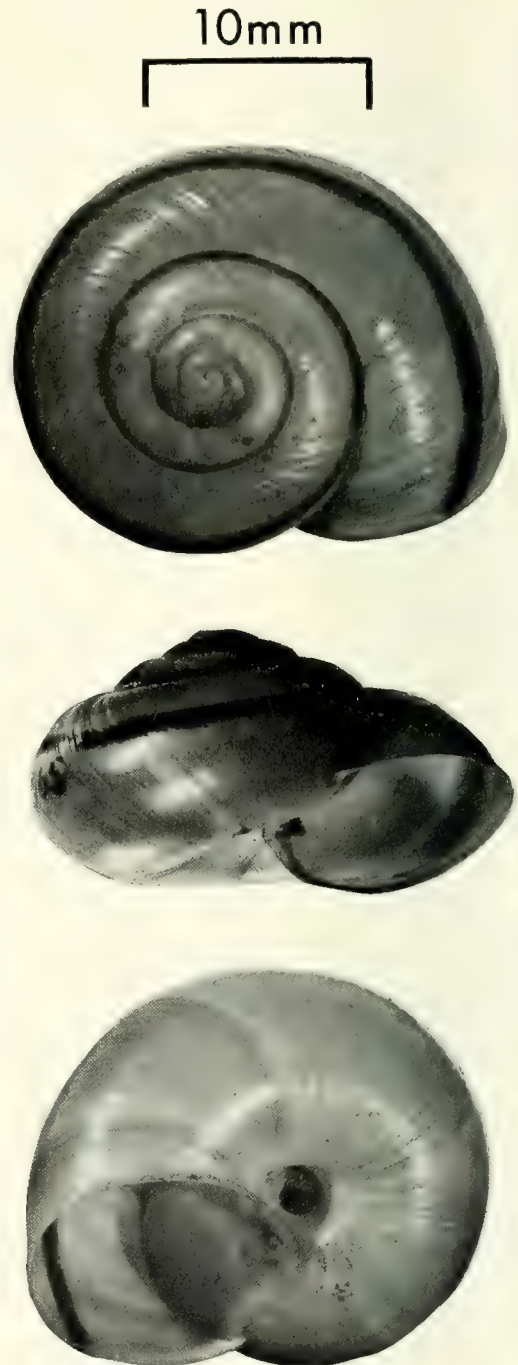
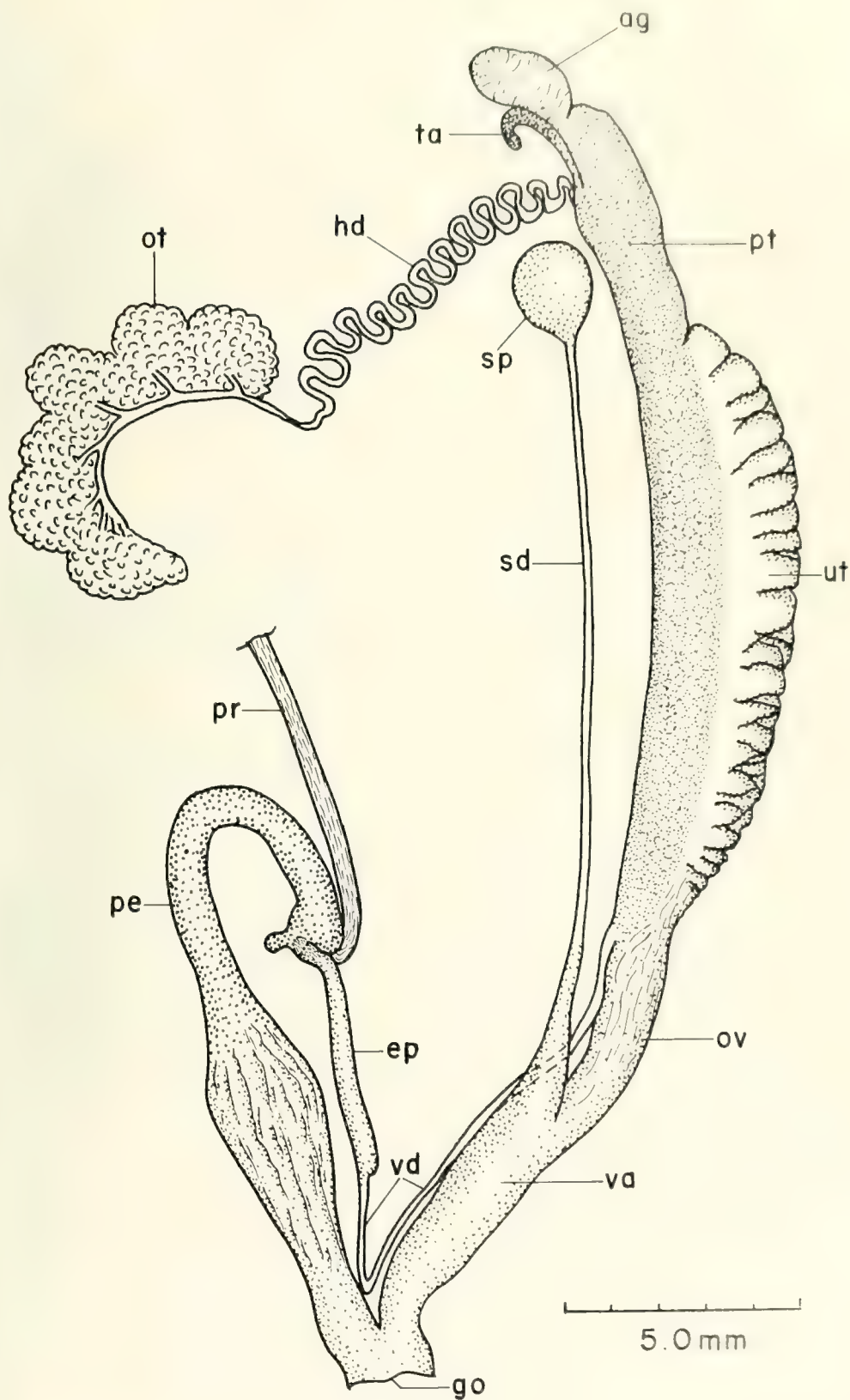


Figure 2. *Sonorella imitator*, new species, three views.

Figure 3. *Oreohelix grahamensis*, new species. Genitalia drawing made from projection of stained whole mount. See figure 1 for key to abbreviations.



Height of holotype 12.0, diameter 21.8, umbilicus 3.0. Average of 17 paratypes: Height 12.2, diameter 21.9, umbilicus 3.0.

Genitalia.—The penis (Fig. 1) is about equal in length to the diameter of the shell and contains a large verge nearly as long as the penis. The verge gradually widens to a blunt distal end. Penis sheath short, penial retractor muscle inserted at the junction of the penis and epiphallus, epiphallus about half the length of the penis and bears at its proximal end a very short epiphallic caecum which is adnate to the adjacent portion of the vas deferens, oviduct very short. Measurements of genital structures: penis 20.8, penis sheath 5.4, verge 18.1, epiphallus 9.3, epiphallic caecum 1.3, penial retractor 7.4, vagina 12.5, oviduct 2.8, spermathecal duct 15.5, spermatheca 2.9×2.9 , atrium 1.4.

Type Locality.—South slope of Mt. Graham, Pinaleno Mountains, Graham Co., Arizona; along "Swift Trail" highway, on north side, at a point 20.7 road miles from its beginning at US highway 666; elevation ca. 9000 feet, collectors M. L. Walton and W. O. Gregg, 21 April 1954.

Type Material.—Holotype, Natural History Museum of Los Angeles County No. 1154. Paratypes: California Acad. Sci., Dept. Geol. No. 12948, San Diego Nat. Hist. Museum, invertebrate type coll. 2545, and private collections of S. S. Berry 31923, W. O. Gregg 8755, W. B. Miller 5357, and M. L. Walton 9279.

Remarks.—On four paratypes which apparently represent senile specimens the peristome is slightly thickened and the parietal callus is moderately thickened. These snails were associated with *Sonorella grahamensis* Pilsbry, from which they are indistinguishable on casual examination. A more careful examination reveals that they fall into two separate size groups, *S. grahamensis* with an average diameter of 19.2 (14 specimens measured), *S. imitator* 21.9 (average 17 paratypes). The latter has a more expanded body whorl which is more flattened above. The penial length of *Sonorella imitator* is approximately equal to the width of the shell; it has a long, robust, blunt-tipped verge occupying nearly the entire length of the penis cavity, whereas *S. grahamensis* has a penis about half as long as the diameter of the shell with a shorter verge which tapers to an acute tip. The oviduct is short in *S. imitator* whereas that of *S. grahamensis* exceeds the length of the verge. The genital anatomy of *S. imitator* closely resembles that of *S. ambigua* Pilsbry and Ferriss and *S. ambigua verdensis* Pilsbry, but the shell sculptures are considerably different. Accordingly, the authors consider the similarity of genital anatomy to be simply a case of convergent evolution.

Sonorella imitator has also been found on Heliograph Peak in the Pinaleno Mountains (Bequaert and Miller, The Mollusks of the Arid Southwest, p. 117, 1973) where it is relatively common, in association with *S. grahamensis*, at the 10,000 foot level. At lower elevations, however, such as along Wet Creek at the 6300 foot level where *S. grahamensis* is abundant, *S. imitator* is absent. It is apparently restricted to the high elevations of the Pinalenos, ca 9000 feet and above.

FAMILY OREOHELICIDAE

Oreohelix grahamensis, new species

Figures 3 and 4

This name was cited as a nomen nudum for a subspecies of *Oreohelix concentrata* (Dall) by Bequaert and Miller, The Mollusks of the Arid Southwest, p. 127, 1973.

Diagnosis.—A moderate-sized species of the *O. yavapai*-group, with closely set spirals on the body whorl, rather prominent lines of growth, and a prominent cornuate process at the proximal end of the penis.

Description of Holotype.—Shell of moderate size, low-conic, widely umbilicate. Whorls five and one half, gradually increasing in size, convex above and below the periphery which is rounded on the last three fourths of the body whorl, a slight keel persisting in the first quarter of the body whorl. The last quarter of the body whorl descends slightly below the strongly keeled periphery of the penultimate whorl. Peristome subcircular, simple, with a thin parietal callus. Aperture lying at an angle of about 45 degrees with the vertical axis of the shell. All whorls visible in the umbilicus which is contained about four times in the greater diameter of the shell. Embryonic shell consists of two and one eighth whorls and is about 4 mm in diameter. First whorl smooth (eroded); traces of growth lines appear on the second whorl at somewhat irregular intervals and continue over the remainder of the shell. Fine spirals appear on the third whorl and continue nearly to the aperture. These spirals are closely set and regular on portions of the shell whereas at intervals they are interrupted by lines of growth; are less closely spaced over the rounded base of the body whorl and are clearly visible in the umbilicus. The coiling is somewhat irregular and in places the suture descends beneath the acute keel of the earlier whorl. On portions of the shell there are traces of a peripheral cord.

Color light snuff brown above, much lighter on the base, with a chestnut band about 1 mm wide above the periphery and another band of the same color

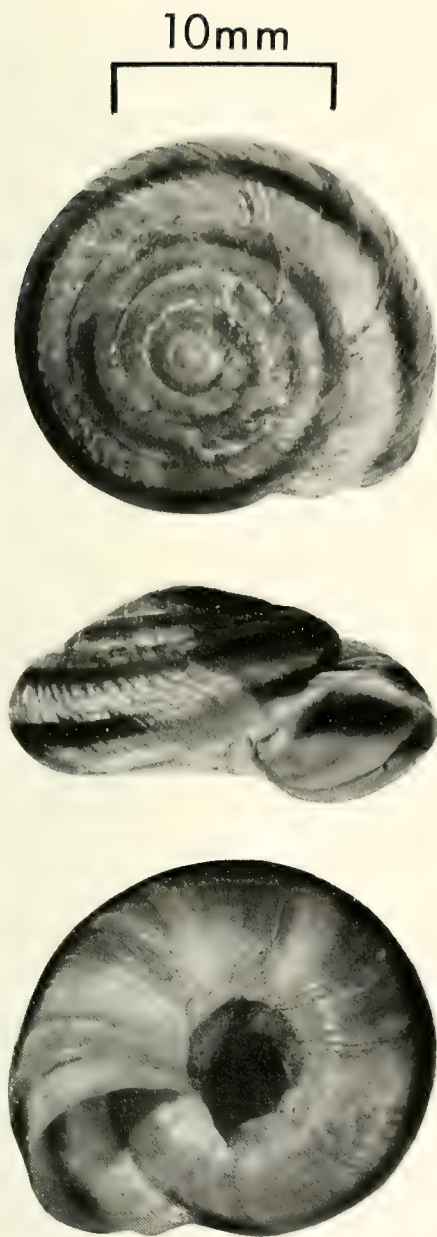


Figure 4. *Oreohelix grahamensis*, new species, three views.

and somewhat wider just below the periphery. Height 10.8, diameter 20.0, umbilicus 5.0.

On uneroded specimens the spirals appear on the last half of the second whorl and the radial lines appear on the first whorl. On some specimens the peripheral cord is continuous though variable.

Genitalia.—Internally ribbed portion (Fig. 3) is more than half the total bulbously expanded; epiphallus spindle-shaped, half the length of the penis. In stained and cleared specimens, the distal end of the epiphallus protrude into the upper end of the penis giving the appearance of a short verge. On the opposite side of this verge-like structure, the proximal end of the penis bears a prominent cornuate projection. These characters of penis and epiphallus are constant in all five anatomies examined. Albumen gland rather small; "talon" well-developed, black. Measurements of genital structures: penis 21.4, internally ribbed portion 12.0, epiphallus 9.1, penial retractor 8.8, vagina 6.6, oviduct 5.6, spermathecal duct 21.5, spermatheca 1.1×1.5 .

Type Locality.—South slope of Mt. Graham, Pinaleno Mountains, Graham Co., Arizona; along "Swift Trail" highway, on north side, at a point 20.7 road miles from its beginning at US highway 666; elevation ca. 9000 feet, collectors M. L. Walton and W. O. Gregg, 21 April 1954.

Type Material.—Holotype, Natural History Museum of Los Angeles County No. 1155. Paratypes: California Acad. Sci., Dept. Geol. No. 12947, Field Museum Nat. Hist. 109587, San Diego Nat. Hist. Museum, invertebrate type coll. 2546, and private collections of S. S. Berry 31922, W. O. Gregg 7038, W. B. Miller 4831, M. L. Walton 6844.

Remarks.—The characteristics of the penis place *O. grahamensis* in the *Oreohelix yavapai*-group of *Oreohelix sensu stricto* (Pilsbry, Acad. Nat. Sci. Philadelphia, Monograph 3, vol. 1(1): 573, 1939). *Oreohelix grahamensis* is most closely related to the *O. concentrata*-complex. From typical *O. concentrata* (Dall), *O. grahamensis* is distinguished by its wider umbilicus, more elevated spire, spiral striation and uniformity of coloration.

Bequaert and Miller (The Mollusks of the Arid Southwest, p. 127, 1973) considered that the populations of *Oreohelix* from the Pinaleno Mountains were only subspecifically distinct from *Oreohelix concentrata* populations in the Huachuca Mountains. Careful comparison of anatomical and shell features as well as consideration of prolonged and extensive geographical isolation have convinced the authors that the genetic heterogeneity which has developed between the populations of these two mountain ranges is most probably sufficient to cause reproductive isolation. Accordingly, *Oreohelix grahamensis* is considered to be a distinct species.

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OBSERVATIONS ON THE LITHODID CRABS OF PERÚ, WITH DESCRIPTION OF TWO NEW SPECIES

JANET HAIG¹

ABSTRACT: Eight species of Lithodidae (Crustacea, Decapoda, Anomura) are reported from deep water off Perú. Two are described as new and a third is illustrated for the first time. The other five species, which were briefly cited from Peruvian waters (del Solar, 1972), are discussed in more detail. Attention is drawn to morphological changes that take place with growth in family Lithodidae. Distribution of the tropical component of the west American lithodids is discussed.

The Lithodidae are a family of anomuran crabs, some of them of large size, which inhabit the littoral zone and depths to at least 2400 m. The family comprises more than 50 species, including such economically important forms as the Alaska king crab, *Paralithodes camtschaticus* (Tilesius), in the north Pacific, and the centolla, *Lithodes antarcticus* Jacquinot, off southern Chile and Argentina. Until recently no lithodids were known from Peruvian waters.

In recent years the Instituto del Mar del Perú (IMARPE) has been conducting investigations in deep water, particularly on crustaceans of potential economic importance. Since late 1970 E. M. del Solar, scientific advisor for IMARPE, has collected material of eight species of Lithodidae aboard "SNP-1," "Wiracocha," and the Japanese trawler "Challua japic." Samples of these, which were sent to me for identification by del Solar, form the basis of this report.

Two of the species were previously undescribed. A third was described by Benedict (1895) from a specimen collected at an unspecified locality by the U.S. Fisheries vessel "Albatross"; it is illustrated for the first time in this paper. The other five species were described by Faxon (1893) from material collected by the "Albatross" in the eastern Pacific between 07°31'30" N and 05°26'20" N; they were listed, with the first Peruvian records, by del Solar (1972).

The presence of Lithodidae in Perú had been recognized earlier on the basis of unidentified fragments taken from the stomach of "cachalotes" (sperm whales). A ninth Peruvian species is represented by legs and part of the carapace of one such specimen, which is housed in a whaling museum at Tierra Colorada to the south of Paita; del Solar believes it to be a *Lithodes* (del Solar, 1972: 6, and pers. comm.). I have seen a photograph of this crab and agree that it bears a general

resemblance to *Lithodes*. However, examination of the rostrum (if present) and the abdomen might prove it to belong to *Neolithodes*. *Neolithodes diomedea* (Benedict) is reported from Chile and from México and is therefore to be expected in Peruvian waters.

Measurements given in this report, except where there is a statement to the contrary, refer to the length of the carapace. All measurements were taken to 0.5 mm using a dial caliper. Specimens, including holotypes of the two new species, are in the collections of the Allan Hancock Foundation (A. H. F.). This paper is contribution No. 351 from the Allan Hancock Foundation.

Lithodes Latreille, 1806

Lithodes Latreille, 1806: 39. Type species by monotypy: *Cancer maja* Linnaeus. Bouvier, 1896: 10, 20.

Carapace spiny; rostrum generally prominent and armed with spines. Antennal acicle (scaphocerite) either well developed, rudimentary, or lacking. Walking legs considerably longer than greatest width of carapace. Second (basal) abdominal somite with median plate fused to lateral plates, and usually with laterals fused to marginal plates; on abdominal somites 3-5, median plate replaced by a membranaceous area covered with calcified platelets; lateral plates of somites 3-5 distinct and paired; marginal plates of somites 3-5 distinct and variable in number, present on both sides in males, on right side only in females.

Lithodes panamensis Faxon, 1893

Lithodes panamensis Faxon, 1893: 166; Faxon, 1895: 50, pl. 10 figs. 1, 1 a-c; Bouvier, 1896: 24; del Solar, 1972: 5, 14.

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Diagnosis: Carapace covered with low, warty protuberances; two pairs of spines on gastric region, two spines on each branchial region, a pair on cardiac and a pair on intestinal region; lateral spines consisting of outer orbital, anterolateral, hepatic, and three branchials. Gastric and branchial regions very convex, defined by deep depressions. Rostrum strongly inclined upward, terminating in a median and two lateral spines; ventral process long but not visible in dorsal view. Antennal acicle long, rudimentary, or absent. Abdominal plates covered with low tubercles; basal (second) somite with a distinct suture on each side separating marginal plate from fused median and lateral plates.

Previous records: 07°31'30" N, 79°14' W, 458 fms [837 m] (Faxon, 1893, 1895). 03°48' S, 81°22' W, 680 m; 07°59' S, 80°22' W, 760–800 m; latitude of Pisco [13°44' S], from stomach of a sperm whale; 17°34' S, 71°55' W, 850 m (del Solar, 1972).

Material examined: Ovigerous female; off Perú, 07°59' S, 80°22' W; 760–800 m, hard bottom; November 1971; E. M. del Solar on trawler "Challua japic."

Measurements: Length of carapace excluding rostrum, 100 mm; maximum width of carapace excluding lateral spines, 108 mm; length of right, third walking leg: merus, 78 mm; carpus, 44 mm; propodus, 70.5 mm; dactyl, 45.5 mm.

Remarks: My specimen agrees well with the description and illustration of the holotype, a female 79 mm long excluding the rostrum. A few minor differences were noted. The three terminal rostral spines are more elongate than the rostral spines of the type; the proximal portion of the rostrum is also longer and advanced beyond the eyestalks. A pair of small spines on the cardiac region of the carapace was not mentioned by Faxon, although his illustration, perhaps erroneously, shows a median spine in that area. The lateral hepatic spines are much larger than they appear in the illustration of the holotype. On each antennal peduncle there is a rudimentary, conical acicle, instead of the long, slender one occurring on the right peduncle in the type.

A specimen collected by del Solar at 17°34' S, has a carapace 190 mm long and measures 970 mm between the tips of the extended legs (del Solar, 1972: 14).

Lithodes wiracocha, new species

Figure 1

Lithodes n. sp.: del Solar, 1972: 14.

Description: Carapace a little longer than broad; surface and all margins densely covered with small, sharp spinules, some of the marginal ones tending to

become enlarged. Gastric region bearing short, stout spines, and separated from branchial region by a deep, transverse depression. Cardiac region well defined, with a pair of small spines. Branchial regions separated from cardiac region by deep, oblique grooves; each branchial region with a well developed spine opposite sulcus separating gastric and cardiac regions. Intestinal region with a pair of small spines. Outer orbital angle marked by a long, slender spine; a shorter one at anterolateral angle; a long, strong marginal hepatic spine; three lateral branchial spines, the most anterior one largest, others not much larger than a few enlarged, laterally situated surface spinules.

Dorsal portion of rostrum inclined upward, with two terminal spines and a pair of median lateral spines; proximal half densely covered with minute spinules to base of median spines; ventral process rather short and not visible in dorsal view, covered proximally with minute spinules.

Eyestalks short, somewhat constricted at about middle, and unarmed, with cornea situated laterally and ventrally. Second segment of antennal peduncle with several spines on its outer side, the most distal one large and elongate and reaching end of penultimate (fourth) segment; acicle rudimentary, conical.

Chelipeds subequal in length, but right somewhat stouter than left; small, thornlike spines, disposed in longitudinal rows, on merus, carpus, and chela; spines somewhat enlarged on ventral surface of ischium. Walking legs long and slender; ischium, merus, carpus, and propodus covered on all sides by longitudinal rows of thorny spines, these a little larger dorsally and ventrally; dactyl with several rows of spines reaching almost to tip.

Abdominal plates, and platelets of somites 3–5, densely covered with sharp spinules. Basal abdominal somite with a median pair of small spines; a narrow, spinule-free line on each side in position of suture which separates marginal from fused median and lateral plates in a few species of *Lithodes*, but in this case no actual suture visible. Lateral plates of left side edged with numerous long, sharp spines, many themselves bearing two or three spinules along each side; marginal plates of right side drawn out into still longer compound spines.

Previous records: 03°48' S, 81°22' W, 680 m; 07°59' S, 80°22' W, 800 m (del Solar, 1972).

Material examined: Holotype, ovigerous female. A.H.F. 712; 12 mi. SW Banco de Mancora, Perú; 620 m, mud bottom; 15 March 1971; E. M. del Solar on trawler "Wiracocha."

Measurements: Length of carapace excluding rostrum, 103.5 mm; rostrum, 16 mm; maximum width of carapace excluding lateral spines, 97 mm; length of right, third walking leg: merus, 78 mm; carpus, 48.5 mm; propodus, 79 mm; dactyl, 47 mm.

Etymology: From Tici Wiracocha, the creator god of Inca mythology, and his namesake, the trawler "Wiracocha" aboard which the holotype was col-

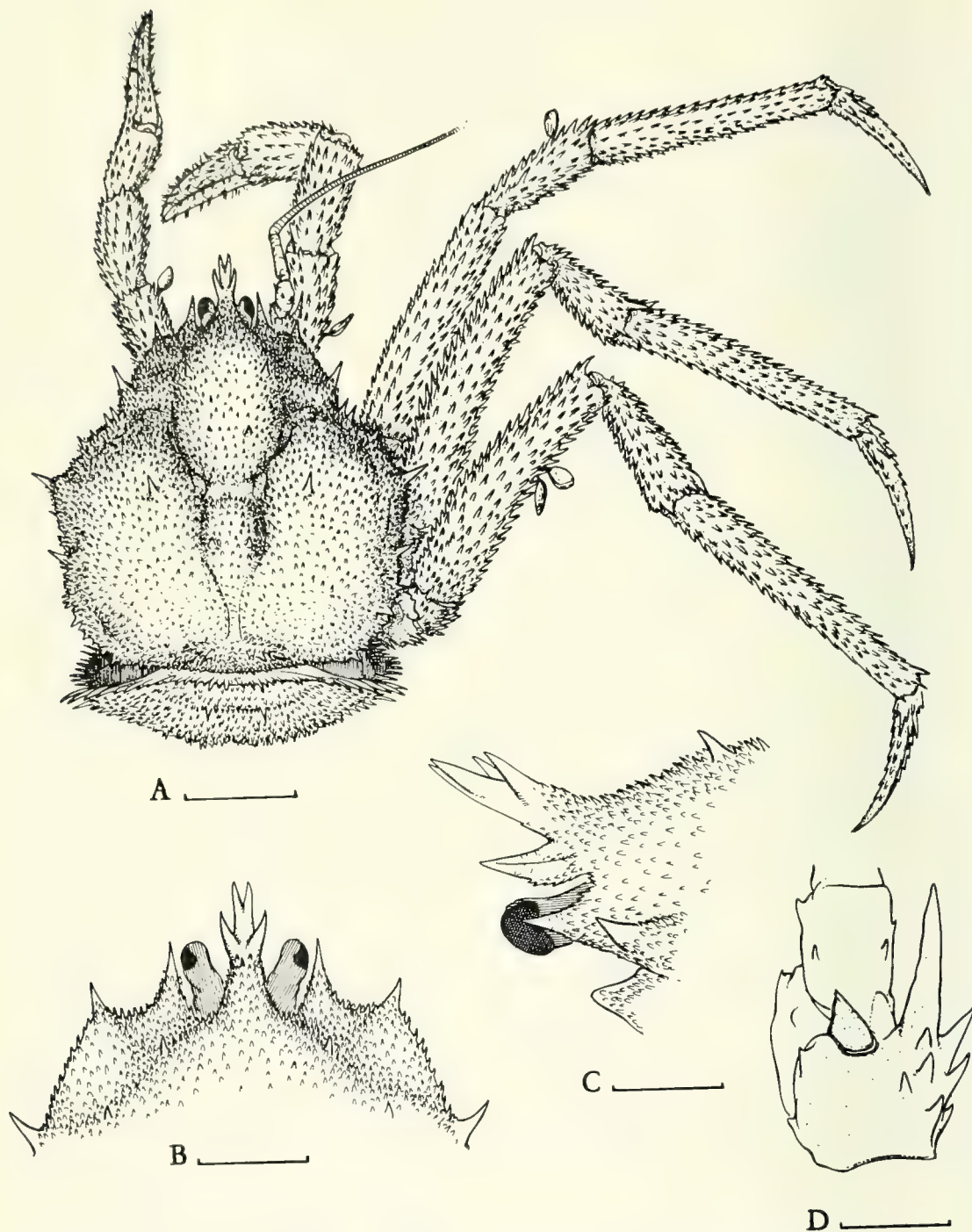


Figure 1. *Lithodes wiracocha*, new species, holotype. A, animal in dorsal view; B, anterior part of carapace, dorsal view; C, same, lateral view; D, right antennal peduncle. Scale A = 30 mm; B = 15 mm; C = 10 mm; D = 5 mm.

lected. To be treated as a noun in apposition to the generic name.

Remarks: This species is distinguished from all other described *Lithodes* by the dense spinulation of the carapace and walking legs. As in *L. murrayi* Henderson (a southern hemisphere species) and *L. tropicalis* A. Milne-Edwards, the rostrum is inclined upward and bifurcate at the tip. *Lithodes panamensis* Faxon also has an upturned rostrum, which however is trifurcate at the tip; Faxon's species is further distinguished from *L. wiracocha* by the pronounced convexity of the gastric and branchial regions of the carapace. The dorsal portion of the rostrum of *L. antarcticus* Jacquinot, which inhabits the southern part of the South American continent, is shorter than the ventral process and the latter is clearly visible in dorsal view.

Several stalked barnacles are attached to the chelipeds and walking legs of the holotype; these have not yet been identified.

Del Solar (1972: 15) reported a specimen with a span of 1.07 m between the tips of the extended legs. An equivalent measurement on the holotype is only 0.58 m.

Paralomis White, 1856

Paralomis White, 1856: 134. Type species by monotypy: *Lithodes granulosa* Jacquinot, Bouvier, 1895: 185; Bouvier, 1896: 12, 21.

Leptolithodes Benedict, 1895: 484. Type species not designated.

Pristopus Benedict, 1895: 486. Type species not designated.

Carapace with spines, tubercles, or other ornamentation according to the species; rostrum short and generally armed with spines. Antennal acicle (scaphocerite) well developed, usually triangular and armed with several spines on margins. Second (basal) abdominal somite fused into a single plate; median plate of somites 3–5 entire; lateral plates of somites 3–5 distinct and paired; in males, marginal plates usually fused to laterals, at least in part, on somite 3 and distinct on somites 4 and 5; in females, marginal plates of somites 3–5 present on right side only.

Paralomis longipes Faxon, 1893

Paralomis longipes Faxon, 1893: 165; Faxon, 1895: pl. 9; Bouvier, 1896: 25; del Solar, 1972: 5, 14. *Leptolithodes longipes*: Faxon, 1895: 48.

Diagnosis: Carapace and abdomen thickly covered with small, blunt tubercles, each encircled by a ring of short, stiff setae; a median spiniform tubercle on anterior part of gastric region; anterolateral and outer orbital spines sometimes enlarged, other laterals (hepatic and three or four branchials) short. Gastric,

cardiac, and branchial regions well defined; tuberculant; grooves defining sides of carapace becoming indistinct posteriorly and not reaching to posterior margin of carapace. Rostrum terminated in a median inferior and two lateral superior spinules; dorsally a median spinule at base of latter and one or two lateral spinules on each side; ventral surface with a protuberance bearing one or two spinules. Antennal acicle with several long, slender spines. Walking legs very long, prismatic, with longitudinal rows of strong, thornlike spines.

Previous records: 05°26'20" N, 86°55' W, 770 fm [1410 m] (Faxon, 1893, 1895). 07°59' S, 80°22' W, 760–800 m; 16°29' S, 73°33' W, 1300 m (del Solar, 1972).

Material examined: Male; off Perú, 07°59' S, 80°22' W; 760–800 m, hard bottom; November 1971; E. M. del Solar on trawler "Challua japic."

Measurements: Length of carapace excluding rostrum, 106 mm; rostrum, 14 mm; maximum width of carapace, 117 mm; length of right, third walking leg: merus, 101 mm; carpus, 56 mm; propodus, 99 mm; dactyl, 76.5 mm.

Remarks: Faxon's description and illustration were based on a male 84 mm long including the rostrum. My specimen differs in only a few details. The outer orbital and anterolateral spines are no larger than the other lateral spines, whereas they are enlarged in the illustrated type. In the Peruvian specimen there are two distinct spinules on each side of the rostrum proximal to the terminal pair of spines. The acicle of the left antenna has six spines and that of the right antenna eight; Faxon described and figured only five spines on an acicle of the male type.

Numerous stalked barnacles are attached to the chelipeds and walking legs.

Paralomis aspera Faxon, 1893

Paralomis aspera Faxon, 1893: 164; Faxon, 1895: pl. 8; Bouvier, 1896: 26; del Solar, 1972: 5, 14. *Leptolithodes asper*: Faxon, 1895: 47.

Diagnosis: Carapace and abdomen thickly covered with papillae or tubercles, each encircled by a ring of stiff setae; no surface spines; a sharp outer orbital and anterolateral spine, and four or five lateral branchial spines. Gastric, cardiac, and branchial regions well defined and prominent. Rostrum short, indistinctly tripartite, multispinose, lower part armed with as many as five spines. Antennal acicle with several spines on each margin and one on both upper and lower side near base. Walking legs of moderate length, stout, densely spinose.

Previous records: 07°06'15" N, 80°34' W, 695 fms [1270 m] (Faxon, 1893, 1895). 03°48' S, 81°20' W, 560 m (del Solar, 1972).

Material examined: Male (juvenile); off Perú; 1971; E. M. del Solar.

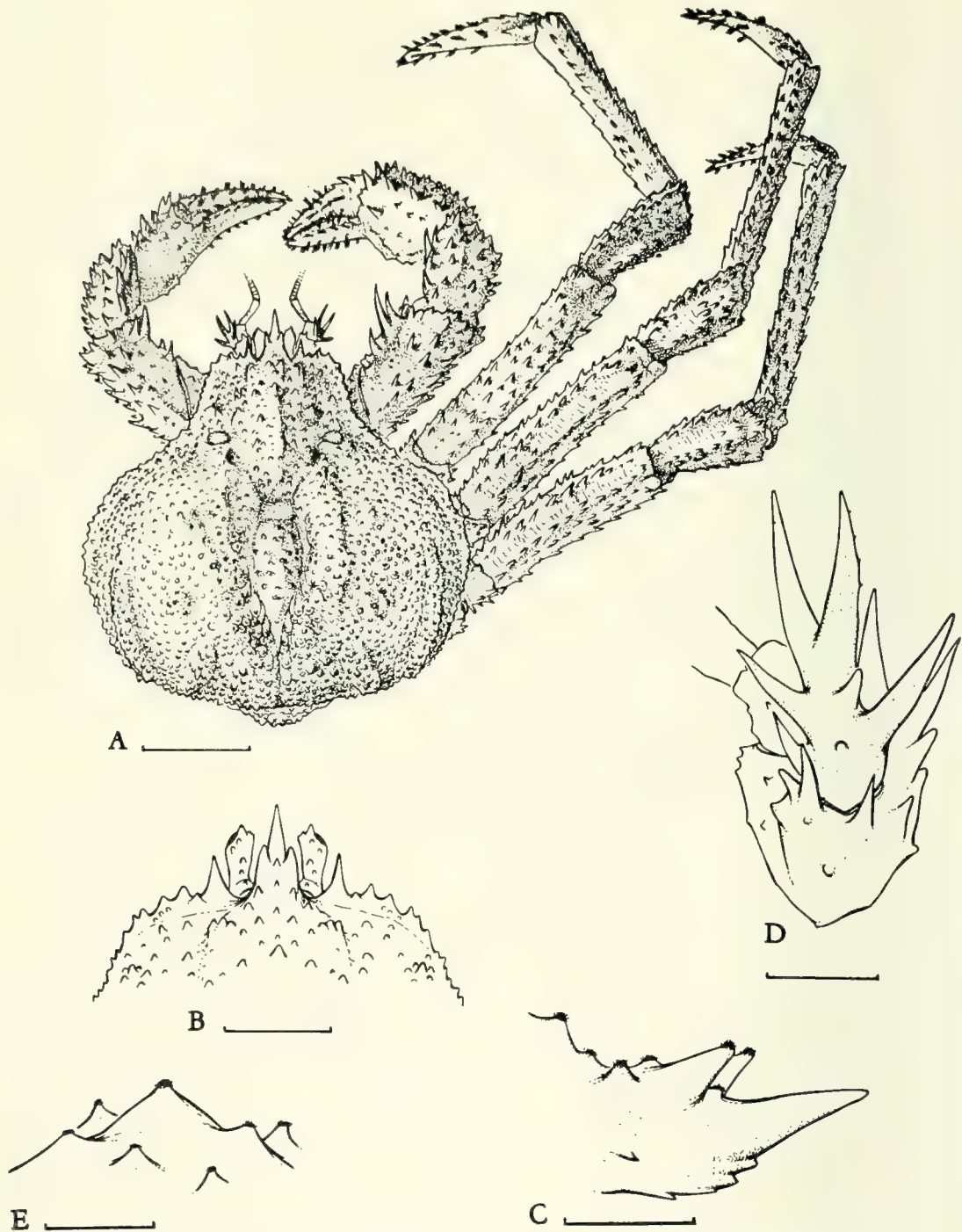


Figure 2. *Paralomis papillata* (Benedict). A, animal in dorsal view; B, anterior part of carapace; C, rostrum, lateral view; D, right antennal peduncle; E, tubercles of carapace. Scale A = 30 mm; B = 15 mm; C = 6 mm; D = 4 mm; E = ca. 7 mm.

Measurements: Length of carapace including rostrum, 75 mm; maximum width of carapace, 75 mm; length of right, third walking leg: merus, 30 mm; carpus, 20 mm; propodus, 27 mm; dactyl, 24 mm.

Remarks: The above diagnosis was derived from the description and illustration of the holotype, a female 122 mm long including the rostrum. The much smaller Peruvian specimen shows striking differences in the surface ornamentation. Each papilla of the carapace and abdomen is raised on a stalk, the whole forming a blunt-tipped (papilliferous) spine; at the base of the papilla is the ring of setae described and figured by Faxon. Toward the carapace margins, and on the chelipeds and walking legs, these spines become more elongate and in many, particularly those of the walking legs, the terminal papilla is tipped with a minute, sharp, corneous spinule. Comparison of a good series of specimens of different sizes would be of interest. Increase of size of individuals is probably accompanied by a gradual reduction of the surface armature from elongate, papilliferous spines bearing setae at the base of the papilla to low, papilliferous tubercles on the carapace and abdomen, these still retaining a ring of setae, and to spines of the usual kind on carapace margins and pereopods.

The rostrum in the Peruvian specimen is multi-spinose as in the type, but shorter and more symmetrical. The eyes have two strong terminal spines, one dorsal and one mesial, extending well beyond the cornea, and there are about twelve smaller spines on the dorsal surface of the eye-stalk. All these spines have a ring of setae below the papillose tip.

Faxon (1893: 165) mentioned that the type was "infested with a huge *Peltogaster* 36 mm in breadth." My specimen also bears a large abdominal sacculinid, in this case 34 mm across.

Paralomis papillata (Benedict, 1895)

Figure 2

Leptolithodes papillatus Benedict, 1895: 485.

Paralomis papillata: Bouvier, 1896: 25.

Diagnosis: Carapace and abdomen thickly covered with small, papilliform tubercles, each bearing stiff setae over summit; no surface spines; outer orbital spine well developed, lateral margins otherwise with small tubercles only. Branchial regions more protuberant than gastric and much more so than cardiac; grooves defining sides of cardiac well defined, meeting at posterior end of this region and continuing as a single deep groove to posterior margin of carapace. Rostrum terminating in a median inferior and two lateral superior spines, latter pair not reaching end

of eyes; ventral surface with an unarmed or short spinulate protuberance. Antennal acicle long, slender spines. Walking legs very prismatic, with longitudinal rows of tubercles and short, stout spines.

Previous records: "Off Lower California, or perhaps south of that region" (Benedict, 1895).

Material examined: Male: off Perú, 06°31' S 81°01' W; 712-744 m, mud and hard sand; 17 May 1971; E. M. del Solar on R/V "SNP-1."

Measurements: Length of carapace excluding rostrum, 100 mm; rostrum, 12 mm; maximum width of carapace, 112 mm; length of right, third walking leg: merus, 64 mm; carpus, 40.5 mm; propodus, 63 mm; dactyl, 55 mm.

Remarks: Del Solar's collection includes two closely allied but distinct species, both of which agree in most respects with the original description of *Paralomis papillata*. Since no illustration of that species was ever published, it was necessary to compare material of both Peruvian forms with the holotype. Photographs of the type, provided by Henry B. Roberts, confirm the identity of the above specimen with Benedict's species.

The type (USNM 18536), which was collected by the "Albatross," is the ecdysal cast of a large male. It is accompanied by the following information: "No label but with spns. from off lower Cal." According to Mr. Roberts the length of the carapace with rostrum is 118 mm, length of the rostrum 10 mm, and breadth of the carapace 130 mm.

My specimen agrees very closely with the type. The carapace is not quite so broad in proportion to its length. The ventral side of the rostral protuberance is minutely denticulate, while in the type this area is practically smooth. Both acicles are similar in structure to the left acicle of the holotype; but in the type specimen the right acicle has a strong terminal spine, and three lateral and two mesial spines which are considerably shorter.

The Peruvian specimen has a few stalked barnacles attached to the walking legs; these are neither so large nor so numerous as those found on the A.H.F. specimens of *Paralomis longipes* and *Lithodes wiracocha*.

Paralomis inca, new species

Figures 3 and 4

Description (Adults): Carapace a little broader than long, covered with tubercles of different sizes each bearing a cluster of very short, stiff setae over summit. Gastric region moderately convex, some of

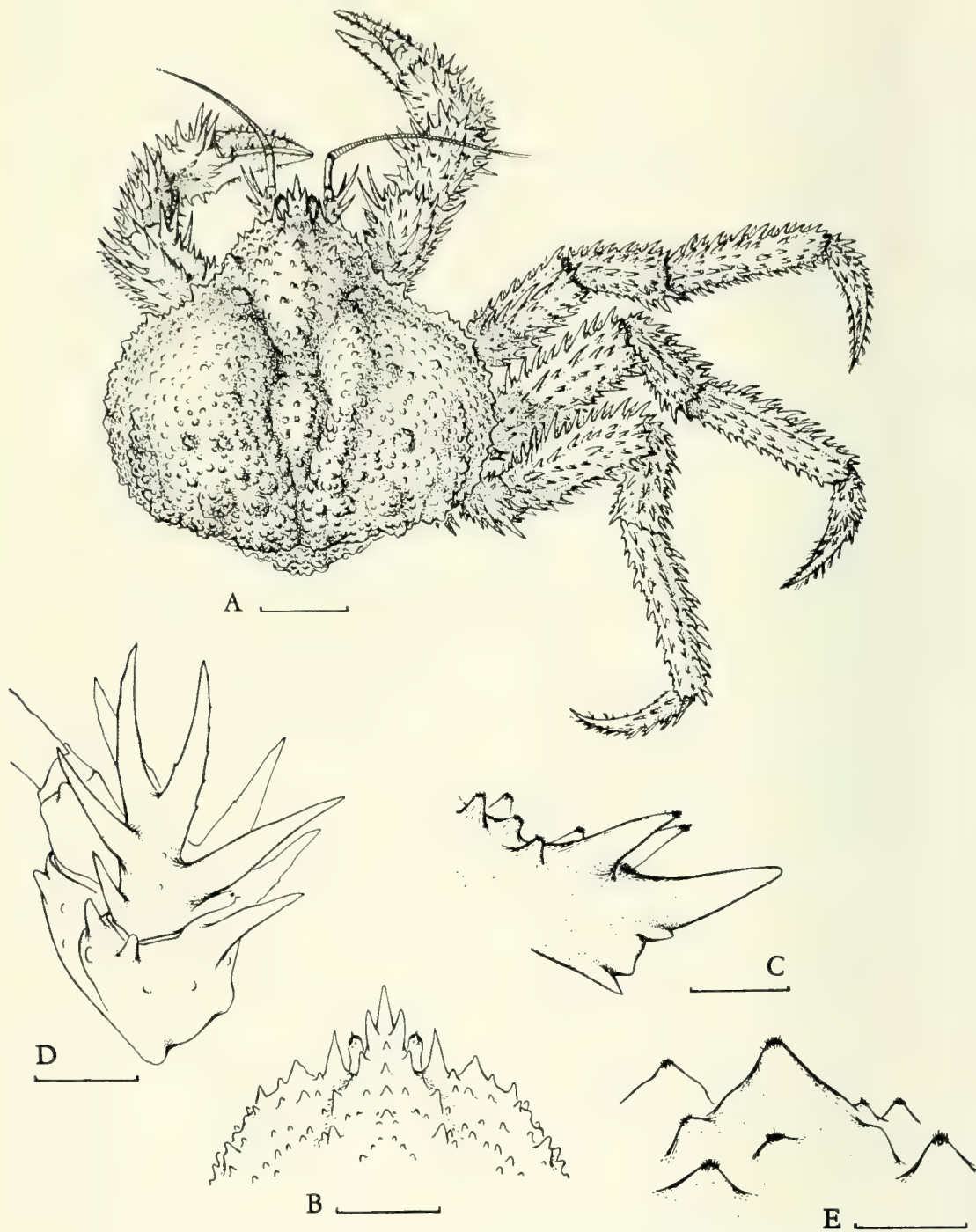


Figure 3. *Paralomis inca*, new species, holotype. A, animal in dorsal view; B, anterior part of carapace; C, rostrum, lateral view; D, right antennal peduncle; E, tubercles of carapace. Scale A = 27 mm; B = 15 mm; C and D = 4 mm; E = ca. 5 mm.

its tubercles small and rounded, others larger, conical, with papilliform or pointed tip (latter type almost spiniform in largest individuals, definitely so in smallest adult). Cardiac region separated from gastric by a deep, rectangular depression; with several conical tubercles and smaller, rounded ones. Branchial regions more protuberant than gastric and much more so than cardiac, separated from latter region by distinct grooves joining at its posterior end and continuing as a single deep groove to posterior margin of carapace; branchials with both large and small tubercles as on other regions, and also with scattered swellings each bearing several small tubercles, a few of latter tending to become spiniform. A number of large, low, pustulous tubercles grouped on posterior part of carapace near midline. Outer orbital angle marked by a sharp spine; lateral margins otherwise with large and small tubercles, some of the larger ones spiniform.

Rostrum terminating in a median inferior and two lateral superior spines, latter pair reaching or surpassing end of eyes; dorsally a median tubercle just proximal to superior pair of spines, and a pointed tubercle on either side at base; underside of inferior spine with a large, distinctly spinulate protuberance.

Eyestalks armed with a few spinules dorsally, largest one terminal and extending beyond cornea. Second segment of antennal peduncle with three or four strong spines laterally, distal one reaching onto terminal segment of peduncle. Acicle with two very strong spines, both appearing to be terminal and of about equal length; also a strong lateral spine and one or two lateral spinules, two strong mesial spines, and two or three very small dorsal spinules.

Chelipeds subequal in length, but right slightly stouter than left. All segments with strong, thorn-like spines, each bearing short setae at tip. Walking legs long, prismatic, with longitudinal rows of strong, thornlike spines and short, pointed tubercles, these setiferous as elsewhere on body.

Abdomen covered with small tubercles, conical or papilliform and setiferous at summit.

(Juvenile): Carapace covered with long, slender spines, each with a tuft of long, flexible setae at and near tip; tip rounded and with a minute corneous spinule. A number of longer, stouter spines occurring as indicated on figure 4A; these sharp-tipped with rudimentary setae. Median area of posterior part of carapace with pustulous tubercles of different sizes; most of these raised on short, stout stalks and thus almost mushroom-shaped. Spinulation of chelipeds and walking legs as in adults, but spines proportionately longer and more slender; terminal setae in a long tuft. Abdomen densely covered with long, slender spines, each tipped with a tuft of long, flexible setae.

Material examined: Holotype, ovigerous female. A.H.F. 718; off Perú, 06°31.5' S, 81°01.5' W; 712–744 m, mud and hard sand; 17 May 1971; E. M. del Solar on R/V "SNP-1."

Paratype, male (juvenile); 12 mi SW Banco de

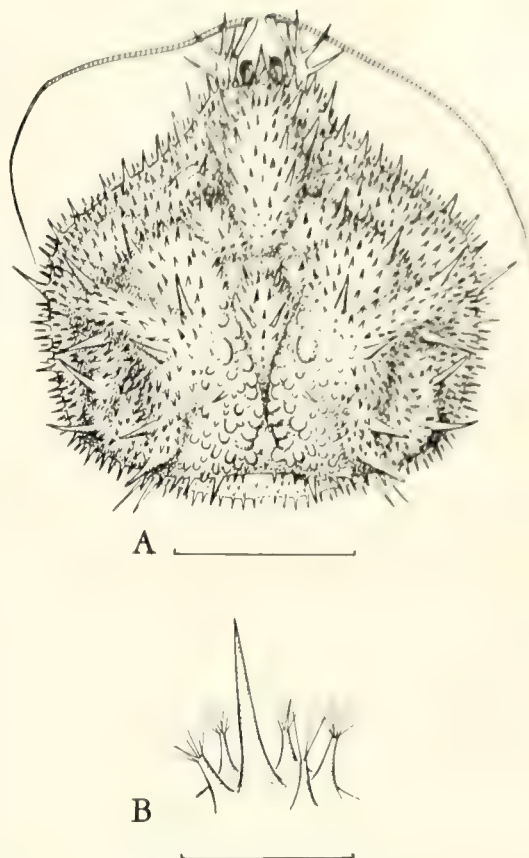


Figure 4. *Paralomis inca*, new species, juvenile paratype. A, carapace; B, carapace spines. Scale A = 30 mm; B = ca. 5 mm.

Mancora, Perú; 620 m, mud bottom; 15 March 1971; E. M. del Solar on trawler "Wiracocha."

Paratypes, male and ovigerous female; off Perú, 07°59' S, 80°22' W; 760–800 m, hard bottom; November 1971; E. M. del Solar on trawler "Challua japic."

Measurements in mm: The measurements for the (holotype), a female, and two males, respectively, are as follows: length of carapace excluding rostrum, (108.0), 93.5, 80.0, 69.0; rostrum, (13.0), 10.0, 10.5, —; maximum width of carapace, (123.0), 109.0, 93.0, 69.0; length of right, third walking leg – merus, (53.0), 50.5, 47.0, 38.0; carpus, (37.0), 35.0, 31.0, 21.5; propodus, (50.0), 48.0, 44.0, 28.5; dactyl, (43.0), 41.5, 40.0, 26.5.

Etymology: As a noun, "Inca" can refer either to an emperor or chief of Perú in the days before the Spanish Conquest, or to a member of the dominant tribe; as an adjective, of or pertaining to the Incas or their empire. Here it is to be considered to be a noun in apposition to the generic name.

Remarks: *Paralomis inca* and the closely allied *P. papillata* share a number of characters, includ-

ing the swollen branchial regions defined by grooves which enclose the sunken cardiac region and extend as a single deep groove to the posterior margin of the carapace; the lack of well developed spines on the lateral margins, aside from the outer orbital spine; armature of the carapace consisting of conical or papilliform tubercles with setae over the summit (not forming a ring below the summit as in *P. longipes* and *P. aspera*); and walking legs long and prismatic, with a row of spines on each longitudinal ridge. This combination of characters distinguishes both species from all other members of the genus. The tubercles of the carapace of *P. inca* are much less uniform in size and shape than they are in *P. papillata*; the lateral superior spines of the rostrum are longer, and the ventral protuberance of the median spine is more strongly spinulate; the walking legs are proportionately shorter, and their spines are longer, slenderer and more numerous.

The 69 mm juvenile male is an ecdysal cast. Many of the spines of the carapace are bent near the tip or in the distal half, with the bent spines oriented in no particular direction; this condition may be due to the soft state of the integument. The dorsal portion of the rostrum is missing. The rather startling difference in appearance between juvenile and adults is duplicated in *P. aspera* Faxon, as I have noted earlier, and probably in other species of *Paralomis* as well. Distinctions between species of this genus are based in large part on the form of the surface ornamentation, but little consideration has been given to changes in this ornamentation that may take place with growth.

Del Solar (1972: 14) listed "*Paralomis* sp." from 06°31' S, 81°01' W in 712–744 m. This record might refer to either the new species or *P. papillata*, which were collected together at that locality.

Lopholithodes Brandt, 1848

Lopholithodes Brandt, 1848 [July]: 174. Type species by monotypy: *Lopholithodes mandtii* Brandt.

Echinocerus White, 1848 [November]: 47. Type species by monotypy: *Echinocerus* (*Lithodes*) *cibarius* White [= *Lopholithodes mandtii*].

Ctenorhinus Gibbons, 1855: 48. Type species by monotypy: *Ctenorhinus setimanus* Gibbons [= *Lopholithodes mandtii*].

Echidnocerus: Bouvier, 1896: 12, 21.

Carapace tuberculate, broader than long, anterior part of branchial margin extended laterally to cover base of walking legs; rostrum short, armed with spini-

form tubercles. Antennal acicle (scaphocerite) triangular, with row of spines on margins. Carpus of chelipeds with a prominent lobe on inner margin, sometimes covering mouthparts; chelipeds and walking legs fitting neatly together when folded, and sometimes folding under carapace. Second (basal) abdominal somite fused into a single plate; median plate of somites 3–5 entire; lateral plates of somites 3–5 distinct and paired; in males, marginal plates distinct or fused to laterals on somite 3, distinct on somites 4 and 5; in females, marginal plates of somites 3–5 present on right side only.

Lopholithodes diomedae (Faxon, 1893)

Echinocerus diomedae Faxon, 1893: 164; Faxon, 1895: pl. 7 figs. 3, 3 a, b.

Paralomis diomedae: Faxon, 1895: 46.

Echidnocerus diomedae: Bouvier, 1896: 27.

Lopholithodes diomedae: del Solar, 1972: 5, 14.

Diagnosis: Carapace tuberculate; anterolateral margins irregularly toothed. Rostrum short, with three spines or sharp tubercles, one median inferior and two paired superior. Antennal acicle with four or five spines on each margin. Carpus of chelipeds with inner lobe toothed on margin; outer margin with an unarmed crest. Walking legs longer than chelipeds and longer than greatest width of carapace; on first pair, anterior margin of carpus with an entire crest, of propodus with crest along proximal half and two or three teeth distally; on second and third pairs, carpus and propodus toothed along anterior margin.

Previous records: 07°31'30" N, 79°14' W, 458 fms [837 m]; 07°21' N, 79°35' W, 511 fms [935 m] (Faxon, 1893, 1895). 03°48' S, 81°22' W, 680 m; 10°01' S, 79°10' W, 830 m (del Solar, 1972).

Material examined: Male; off Perú, 10°01' S, 79°05' W; 830 m, hard mud bottom; 19 May 1971; E. M. del Solar on R/V "SNP-1."

Measurements: Length of carapace excluding rostrum, 101 mm; rostrum, 9 mm; maximum width of carapace, 128 mm; length of right, third walking leg: merus, 56 mm; carpus, 38 mm; propodus, 39 mm; dactyl, 47 mm.

Remarks: Faxon described this species from two female specimens. My male differs from the description and illustration of the larger, 64 mm type in having the various articles of the chelipeds and walking legs more elongate.

The genus *Lopholithodes* contains two other species, *L. mandtii* Brandt and *L. foraminatus* (Stimpson), both from the temperate north Pacific. In those species the walking legs are about as long as the chelipeds and shorter than the greatest width of the carapace, and all the pereopods are modified to fold under the carapace, the inner marginal crest of the carpus of the chelipeds covering the mouthparts and the whole forming a boxlike structure. In *Lopholithodes diomedae*

the legs are long and do not fold beneath the carapace, and the chelipeds are elongate enough so that the carpal crest cannot cover the mouthparts. In the Peruvian specimen, the first male to be reported, the marginal plates of the third abdominal somite are almost completely fused with the lateral plates. In this character *L. diomedae* is closer to *L. foraminatus* than to *L. mandtii*, in which the marginal plates are distinct on the third abdominal segment of males.

In the original description, Faxon (1893) placed this species in *Echinocerus* and compared it with *E. foraminatus* Stimpson; later (1895) he changed his mind as to its affinities and allied it with *Paralomis granulosa* (Jacquinot). Bouvier (1896) retained it in *Echinocerus* (with spelling *Echidnocerus*) alongside *E. cibarius*, *E. setimanus* (both = *mandtii*) and *E. foraminatus*. *Lopholithodes* has since been shown to have priority over *Echinocerus*, so the correct name for Faxon's species is *Lopholithodes diomedae*. It was reported for the first time in this combination by del Solar (1972), for whom I had provided an identification.

Glyptolithodes Faxon, 1895

Glyptolithodes Faxon, 1895: 42. Type species by monotypy: *Rhinolithodes cristatipes* Faxon.

Carapace with a large, conical prominence on gastric region, one on each posterolateral margin, and two on posterior margin; a prominent, crescentic, rounded ridge on each branchial region, enclosing cardiac region in a deep fossa; rostrum conical, with a short, laterally compressed ventral process. Antennal acicle (scaphocerite) triangular, margins spined. Walking legs flattened, nearly spineless, margins lobed or dentate. Second (basal) abdominal somite fused into a single plate; median plate of somites 3–5 entire; lateral plates of somites 3–5 distinct and paired; in males, marginal plates partially fused to laterals on somite 3 and distinct on somites 4 and 5; in females, marginal plates of segments 3–5 present on right side only.

Glyptolithodes cristatipes (Faxon, 1893)

Figure 5

Rhinolithodes cristatipes Faxon, 1893: 163; Faxon, 1895: pl. 7 figs. 2, 2 a–c; Bouvier, 1896: 27.

Glyptolithodes cristatipes: Faxon, 1895: 43; del Solar, 1972: 5, 13.

Rhinolithodes (*Glyptolithodes*) *cristatipes*: Bahamonde, 1967: 3, pl. 1.

Diagnosis: Carapace broader than long, covered with small granules; outer orbital and anterolateral angles with a small, blunt tooth; anterolateral (an-

terior branchial) margin with a few conical teeth; prominences on carapace as in figure 5. **Generic diagnosis:** cardiac fossa open posteriorly. Rostrum short, conical, unarmed dorsally. Gastric process denticulate anteriorly, not visible in lateral view. Antennal acicle with a terminal spine and two to four spinules on each margin. Carpus of chelipeds flattened, outer margin cristate and sometimes cut into two or three lobes, inner margin with crest expanded and cut into dentiform lobes or armed with several sharp teeth. Walking legs longer than greatest width of carapace in adults; anterior margin of merus, carpus, and propodus cristate, crest entire or cut into two to several lobes; posterior margin of those articles dentate. Abdomen tuberculate.

Previous records: 07°09'45" N, 80°50' W, 322 fm [590 m] (Faxon, 1893, 1895). S of Banco de Mancora, Perú, 400 m; 03°51' S, 81°18' W, 800 m; 07°42' S, 80°26' W, 693 m (del Solar, 1972). Off Iquique, Chile, depth unrecorded; 25°11' S, 70°31' W, 245–266 m (Bahamonde, 1967).

Material examined: Female (juvenile); S of Banco de Mancora, Perú, 03°51.3' S, 81°18.2' W: 795–800 m, mud bottom; 11 January 1971; E. M. del Solar on R/V "SNP-1."

Female; off Perú, 06°31.5' S, 81°01.5' W: 712–744 m, mud and hard sand; 17 May 1971; E. M. del Solar on R/V "SNP-1."

Male; off Puerto Chicama, Perú, 07°42' S, 80°26' W; 693 m, rocky bottom; 2 March 1971; E. M. del Solar on R/V "SNP-1."

Measurements: Length of male carapace excluding rostrum, 79.5 mm; rostrum, 6 mm; maximum width of carapace, 98 mm; length of right, third walking leg: merus, 44.5 mm; carpus, 28 mm; propodus, 38 mm; dactyl, 37.5 mm. Length of female including rostrum, 89.5 mm. Length of juvenile including rostrum, 27 mm.

Remarks: The original description of this species was based on a juvenile male specimen. The juvenile collected by del Solar is larger than the 16.5 mm holotype, but agrees closely with it. Adults, on the other hand, show a number of differences, some of which were pointed out by Bahamonde (1967), who reported six large specimens from off Iquique and Taltal, Chile. The carapace is broader than long instead of about as long as broad; the setae which decorate its lateral prominences in juveniles are absent in adults. There are three or four spines, instead of two, on each margin of the antennal acicle. The walking legs are much longer than the carapace width, and the various articles of these legs are proportionately more elongate than they are in juveniles.

On the illustrated specimen (Fig. 5A) the artist has depicted an abnormally small (probably regenerating) third walking leg. The third walking

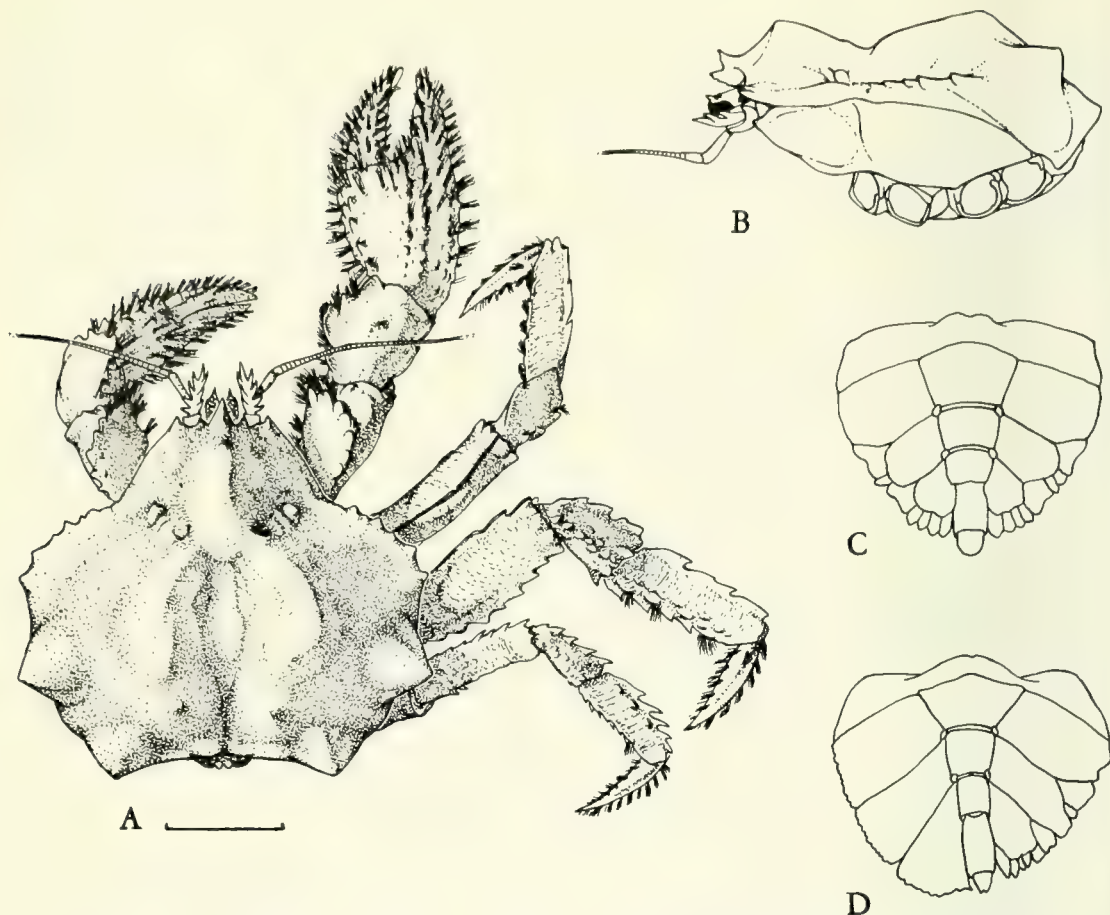


Figure 5. *Glyptolithodes cristatipes* (Faxon). A, male in dorsal view; B, same specimen, carapace in lateral view; C, abdomen of male; D, abdomen of female. Scale A = 30 mm.

legs are normally about the same size as the other two pairs.

The abdomen of the 89.5 mm female bears a sacculinid 45 mm across.

In his original description of this species, Faxon (1893) referred it provisionally to *Rhinolithodes* Brandt. Later he examined material of *R. wosnessenskii* Brandt and concluded that the two species are generically distinct. Characters by which he distinguished *Glyptolithodes* from *Rhinolithodes* (Faxon, 1895: 43) include the form of the rostrum and legs and of the cardiac region, which is elevated and spherical in *R. wosnessenskii*, the type species of *Rhinolithodes*. Bouvier (1896), who evidently did not know of Faxon's 1895 work, failed to mention *Glyptolithodes* and retained *G. cristatipes* in *Rhinolithodes*, a genus characterized by having the marginal plates of abdominal segments 3–5 com-

pletely fused with the corresponding lateral plates (Bouvier, 1895: 187; 1896: 21). This is true of both sexes, as I have confirmed by examination of a male and a female *R. wosnessenskii* in the collections of the Allan Hancock Foundation. The very different structure of the abdomen in *G. cristatipes* (Fig. 5 C, D) confirms Faxon's opinion that his species belongs to a separate genus.

REMARKS ON DISTRIBUTION

Bouvier (1896) showed that the Lithodidae, a family adapted to cold and temperate waters, originated in the North Pacific and underwent tropical submergence during its migration southward along the Pacific coast of the Americas. On that coast it re-emerged at about 42° S, from which latitude southward it is represented by

Lithodes antarcticus Jacquinet and *Paralomis granulosa* (Jacquinet) in the littoral and to depths of about 150 and 100 m, respectively. The deep-water, tropical component of this fauna first became known when Faxon (1893) described *Lithodes panamensis*, *Paralomis longipes*, *P. asper*, *Lopholithodes diomedae*, and *Glyptolithodes cristatipes* from between 07°31'30" N and 05°26'20" N, in 590 to 1410 m. Shortly afterwards, Benedict (1895) described *Paralomis papillata* from a specimen collected at an unrecorded depth and an uncertain locality, probably off México.

Rathbun's (1910) pioneer compilation of the decapod Crustacea of Perú included no Lithodidae, because at that time practically no exploration of the deep sea had been made in Peruvian waters. This situation continued to exist until very recently, when the investigations of IMARPE (del Solar, 1972) yielded all five of Faxon's species as well as *Paralomis papillata* (Benedict) and the two new species described in the present report. *Glyptolithodes cristatipes* was recorded from Chile at 25°11' S by Bahamonde (1967), who noted that fragments of two undetermined species, a *Paralomis* and a *Leptolithodes* [= *Paralomis*], have been taken from stomachs of sperm whales captured in Chilean waters. *Lithodes panamensis* and *Glyptolithodes cristatipes* are known to occur off northern México (unpublished records). Thus, although much deep-water exploration of the Pacific American coast remains to be done, a general picture of the "tropical component" of the Lithodidae is becoming clearer: it consists of at least eight benthonic species and, considered as a unit, reaches its northern limit in tropical México but penetrates the temperate Chilean waters to the south.

Faxon (1895: 51) reported small, indeterminate juveniles of "two more species of *Lithodes*" from the collections of the "Albatross" off tropical western America. One of these, taken between 16°33' N and 0°04' S in 1207 to 1847 m, belongs to *Neolithodes* A. Milne-Edwards and Bouvier, 1894. *Neolithodes diomedae* (Benedict) was described off southern Chile from 42°36' S and 45°35' S in 2454 and 1920 m, respectively, and has since been reported from 23°39' N in 1382 m (Parker, 1964: 163). Until more is learned about the genus in the eastern Pacific, it is impossible to say whether Faxon's specimens belong to *N. diomedae* or to another, as yet undiscovered form. As I complete the final draft of this report, E. M. del Solar informs me (pers. comm.) that he has found a juvenile *Neolithodes* from Peruvian waters, and that he intends to

investigate its status and that of other *Neolithodes* taken in Perú from the stomachs of sperm whale (see introduction).

A deep-water species of *Lithodes* and *Paralomis* occur in the northeast Pacific and at least as far south as southern California: they are not well known from the southern part of their range, which may overlap to some extent the range of the tropical group of lithodids. Faxon's second undetermined *Lithodes* (Faxon, 51, pl. 10 fig. 2), a juvenile collected at 21°19' N, is perhaps a very small specimen of *L. couesi* Benedict, whose reported range is Bering Sea to San Diego, California.

ACKNOWLEDGMENTS

I am pleased to acknowledge the help I received from several sources, without which this study could never have been completed. Enrique M. del Solar not only furnished the specimens on which it was based, but provided information on additional Peruvian material as well as constant encouragement. Henry B. Roberts provided photographs and information on the holotype of *Paralomis papillata* (Benedict). A subvention from the Sociedad Nacional de Pesquería of Lima, Perú, made possible the illustrations, which are the work of Jerry J. Battagliotti.

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RANGE EXTENSIONS FOR SOME CALIFORNIA MARINE ISOPOD CRUSTACEANS

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ABSTRACT: New range extensions are given for 22 species of California marine isopods. Brief ecological data and intermediate localities are included. *Dynamenella diana* and *Excirolana kincaid* are added to the California fauna. New localities are given for four species previously known only from the type localities.

Numerous collections of marine isopods have been made by the author along the California coast in the past several years. Examination of this and other material has resulted in 22 new range extensions and numerous intermediate localities being recognized. New records were also encountered while curating a portion of the marine isopod collection in the Department of Invertebrate Zoology, California Academy of Sciences

(CAS), the Hopkins Marine Station collection (HMS), Pacific Grove, California (recently transferred to the CAS collection), and from materials sent to the author for identification. Several new records were obtained from a collection of iso-

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pods dredged by the R/V Amigo and the R/V Falcon during a benthic survey of the northern sector of Monterey Bay, California. The survey was conducted by the Moss Landing Marine Laboratory (MLML), Elkhorn slough, California, under contract to the Association of Monterey Bay Area Governments and later under the Sea Grant Program. The sublittoral isopod fauna obtained showed a remarkable resemblance to the southern California fauna reported by Menzies and Barnard (1959). Seven species were collected by the survey, two of which, *Austrosignum* sp. and *Tecticeps convexus* have not been reported from southern California. One species *Bathycopea daltonae* has previously been reported from off San Francisco, California (Loyola e Silva, 1971).

The museum records reported herein may represent temporary non-reproducing populations resulting from introductions by man or from unusual environmental conditions such as the occasional intrusion of warm water into central California from the south. Early records of introduced species are reported to provide possible base dates from which times of introduction and subsequent dispersal along the coast may be judged.

Two species, *Dynamenella diana* and *Excrolana kincaidi* are here added to the California fauna, while four species are reported for the first time outside their type localities.

The specimens upon which the present range extensions are based have been deposited in the collections of the Department of Invertebrate Zoology, California Academy of Sciences or the Moss Landing Marine Laboratory (MLML benthic survey material only).

SUBORDER ANTHURIDEA

FAMILY ANTHURIDAE

Haliophasma geminata Menzies and Barnard
Previous distribution: Southern California coastal shelves and slopes, 9.2 to 512.4 m; Santa Catalina Island, 73.2 to 122.6 m; Santa Rosa Island, 14.6 m (Menzies and Barnard, 1959:19), and San Quintin Bay, Baja California, Mexico (Menzies, 1962:339).

New northern record: Station 1159, SW Rio Del Mar, Monterey Bay, California, 36° 57.1' N. Lat., 121° 56.2' W. Long.; 3 May 1972; MLML benthic survey; dredged in 15 m over grey sand.

Collected from other parts of Monterey Bay at depths ranging from 15 to 65 m by the MLML survey. Bottom sediments varied from grey sand (shallowest stations) to mud (deepest stations).

SUBORDER ASELIOTA

FAMILY JANIRIDAE

Iais californica (Richardson)

Previous distribution: Australia, New Zealand, Singapore, and California from Bodega Bay, Tomales Bay, Bolinas Lagoon, and San Francisco Bay (Rotramel, 1972:193-194), and Newport Bay (Anonymous, 1965:203).

New northern record: Near Samoa, Humboldt Bay, California; 29 April 1972; E. Iverson and R. Talmadge; commensal on the sphaeromid isopod *Sphaeroma quoyana* (= *S. pentodon* Richardson, 1904).

Ianiropsis epilittoralis Menzies

Previous distribution: Dillon Beach, Marin Co., California, and Pacific Grove, Monterey Co., California (Menzies, 1952:150-151).

New southern record: 3.2 miles N Arroyo Laguna Creek, San Luis Obispo Co., California; 5 February 1972; E. Iverson; several specimens from green filamentous algae in the high intertidal.

FAMILY MUNNIDAE

Munna halei Menzies

Previous distribution: Tomales Point, Marin Co., California (Menzies, 1952:134).

New southern record: El Capitan Beach, San Luis Obispo Co., California; 28 December 1971; E. Iverson; numerous specimens from among the spines of the purple sea urchin, *Strongylocentrotus purpuratus*, taken among rocks and debris in the mid-tide zone.

SUBORDER FLABELLIFERA

FAMILY CIROLANIDAE

Excrolana kincaidi (Hatch)

Previous distribution: San Juan Island, Washington (George and Stromberg, 1968:252) to Coos Bay, Oregon (Hatch, 1947:208).

New southern record: Torrance Beach, Los Angeles Co., California; 13 September 1972; E. Iverson; screened from fine wet sand just below the maximum reach of the waves near the high tide mark. The related isopod *E. linguifrons* (Richardson, 1899) was also collected from the same habitat.

Further records: Intermediate localities in California include Drakes Beach (20 July 1969, G. L. Rotramel), and mouth of Bolinas Lagoon, Marin Co. (19 December 1972, John Chapman; Aquatic Park Marina, San Francisco Bay (25 May 1972, D. Behrens); and Princeton Harbor, Half Moon Bay, San Mateo Co. (5 July 1971, E. Iverson and D. Behrens).

FAMILY CYMOTHOIDAE

Lironeca californica (Schioedte and Meinert)

Previous distribution: Alaska (Hatch, 1947:211) to San Pedro, Los Angeles Co., California (Richardson, 1905a:260).

New southern record: Entrada Point, San Quintin Bay, Baja California, Mexico; 23 March 1949; R. R. Harry *et al.*; parasitic on the gills of the Dwarf Surfperch, *Micrometrus minimus*.

Remarks: *Lironeca californica* previously has been reported parasitizing three other species of fish. This is the second member of the family Embiotocidae to be infected.

FAMILY SPHAEROMIDAE

Dynamenella diana (Menzies)

Previous distribution: San Quintin Bay, Baja California, Mexico; Mayaguez Bay, Puerto Rico, and Eniwetok Atoll, Marshall Islands (Glynn, 1970:20).

New northern record: Ventura Yacht Harbor, Ventura Co., California; 20 September 1972; E. Iverson; from fouling on floats and under rocks used as shoring.

Further records: Additional new localities in southern California include Marina Del Rey Harbor (16 September 1972, E. Iverson) and Redondo Beach, Los Angeles Co. (14 September 1972, E. Iverson); Oceanside Harbor (19 September 1972, E. Iverson), and San Diego Bay, San Diego Co. (19 September 1972, E. Iverson).

Exosphaeroma inornata Dow

Previous distribution: Palos Verdes, Los Angeles Co., California (Dow, 1958:93).

New northern record: Bune Point, Humboldt Bay, California, 29 April 1972; E. Iverson; from algae covered rocks.

Further records: A eurytopic species from many additional localities in California between Horse-shoe Cove, Bodega Bay to near Arroyo Laguna creek, San Luis Obispo Co.

Exosphaeroma octoncum (Richardson)

Previous distribution: Monterey Bay, California (Richardson, 1899:836).

New northern record: Tomales Head, Marin Co., California; 1 July 1969; D. Beach and B. Roth; one specimen from the CAS collection.

Gnorimosphaeroma lutea (Menzies)

Previous distribution: Popov Island, Alaska (Menzies, 1954:14) to Oso Flaco Lake, San Luis Obispo Co., California (Eriksen, 1968:5).

New southern record: El Capitan Beach, San Luis

Obispo Co., California; 28 December 1971; E. Iverson; one specimen near the mouth of a small stream, under marine algae cast ashore.

Gnorimosphaeroma noblei Menzies

Previous distribution: Upper region of Tomales Bay, California (Menzies, 1954:21–22), and Urup Island, Kurile Islands, Sea of Okhotsk (Kussakin, 1972:156).

New northeastern Pacific northern and southern records: Near Samoa, Humboldt Bay, California; 29 April 1972; E. Iverson and R. Talmage; numerous specimens from the mud overhang of small channels crossing a *Salicornia* flat and under marine algae at the edge of the flat; and Palos Verdes, Los Angeles Co., California; 13 September 1972; E. Iverson; under rocks in tide pools of the middle tide zone on the semi-protected outer coast.

Sphaeroma quoyana Milne-Edwards

Previous distribution: Australia, Tasmania, New Zealand, and in northeastern Pacific bays: in California: Bodega Bay, Tomales Bay, Bolinas Lagoon, San Francisco Bay (Rotramel, 1972:193–194), San Pedro, Los Angeles Harbor (Johnson and Snook, 1927:287), Newport Bay (Menzies, 1962:340), San Diego Bay (Johnson and Snook, 1927:287), and in Mexico: San Quintin Bay, Baja California (Menzies, 1962:340).

New northern record: Near Samoa, Humboldt Bay, California; 29 April 1972; E. Iverson and R. Talmage; numerous specimens burrowing in the mud banks of the small channels running through the *Salicornia* flat. One dried lot of *S. quoyana* was found in the HMS collection from Humboldt Bay (1931, G. MacGinitie collector). The commensal *Iais californica* is present in both the 1931 and 1972 collections.

Further records: Morro Bay, San Luis Obispo Co., California (24 September 1972, J. Carlton).

Remarks: *Sphaeroma quoyana* (as *S. pentodon* Richardson, 1904) has been reported twice from Alaska, first, under questionable circumstances, by Atwood and Johnson (1924:26) and again by Johnson and Snook (1927:288). These records probably resulted from Richardson including the original description of *S. pentodon* in the reports of the Harri-man Alaska Expedition (1904:214–215). Her description was based on ten specimens collected by Ritter and party at Sausalito, San Francisco Bay. Although several authors have studied the fauna of the upper northeastern Pacific, additional records are not available. Thus the Alaskan records are probably not valid.

Tecticeps convexus Richardson

Previous distribution: Monterey Bay, California (Richardson, 1899:838).

New northern and southern record: 0.5 miles SW

Crescent City Whistle Buoy, California; 13 August 1940; collector unknown; 24 specimens trawled from 31 m; and near Point Conception, Santa Barbara Co., California; 14–17 July 1916; Carl L. Hubbs; both lots are from the CAS collection.

Further records: Additional intermediate localities in California include: 1.5 miles SW off the Mad River (9 August 1940; collector unknown); Horse-shoe Cove, Bodega Head (7 August 1971); J. Carlton; off Doran Beach, Bodega Bay (29 March 1967, A. Kuris and J. Ackeman), and Drakes Bay, Marin Co., (2 March 1936; L. Hertein).

SUBORDER GNATHIIDEA

FAMILY GNATHIIDAE

Gnathia crenulatifrons Mond

Previous distribution: Southern California coastal shelves and slopes, Santa Catalina Island and basin at depths from 9.2 to 1259 m (Menzies and Barnard, 1959:29).

New northern record: Station 1152, south of Point Santa Cruz, Monterey Bay, California; 36° 54.8' N. Lat., 122° 1.0' W. Long.; 20 August 1971; MLML benthic survey; dredged in 37 m over grey sand.

SUBORDER VALVIFERA

FAMILY ARCTURIDAE

Idarcturus allelomorphus Menzies and Barnard

Previous distribution: Point Conception to Laguna Beach, California, and Cortes Bank, SW San Clemente Island, California, at depths from 12.8 to 91.5 m (Menzies and Barnard, 1959:23).

New northern record: Station 1153, SW Soquel Point, Monterey Bay, California; 36° 56.7' N. Lat., 121° 59.2' W. Long.; 21 August 1971; MLML benthic survey; dredged in 35 m over grey sand.

FAMILY IDOTEIDAE

Edotea sublittoralis Menzies and Barnard

Previous distribution: Southern California coastal shelves from Point Conception to the Mexican border at depths from 13.7 to 64 m (Menzies and Barnard, 1959:22).

New northern record: West of Daly City, San Francisco Co., California; 9 September 1972; John Chapman; near a sewer outfall at a depth of 9.8 m.

Further records: Several specimens were collected in the northern sector of Monterey Bay, California by the MLML benthic survey in 12 to 35 m over a sandy substrate.

Idotea (Idotea) rufescens (Fee)

Previous distribution: Gabriola Pass, Departure Bay, Vancouver Island (Fee, 1926:18) to Marin Co., California (Menzies, 1950:170).

New southern record: South of Carmel, Monterey Co., California; 8 January 1967; D. Wabblers; one specimen from the CAS collection.

Remarks: This specimen, an ovigerous female, agrees with the diagnosis given by Menzies (1950:170) except for the apex of the frontal process, which is notched. Similar variation is known from one other eastern Pacific idoteid, *I. (Pentidotea) aculeata*.

Idotea (Pentidotea) montereyensis (Maloney)

Previous distribution: Seabeach, Kitsap Co., Washington (Hatch, 1947:219) to Estero Bay, San Luis Obispo Co., California (Menzies, 1950:187).

New northern and southern records: Boundary Bay, British Columbia; July 1916; F. W. Weymouth; one specimen from the CAS collection; and Pismo Beach, San Luis Obispo Co., California; 23 October 1970; E. Iverson; one specimen from drifting brown algae in the surf.

Idotea (Pentidotea) resecata Stimpson

Previous distribution: Karta Bay, southeast Alaska (Richardson, 1905b:216) to Los Coronados Islands, SW San Diego, California (Miller, 1968:20).

New southern record: At sea in the mouth of the Gulf of California between 23° 12' N. Lat., 106° 29' W. Long., and 23° 3' N. Lat., 109° 31' W. Long.; 3 August 1932; Crocker Galapagos Expedition; one specimen from the CAS collection.

Remarks: In California, *I. (P.) resecata* is commonly found in the intertidal zone among rocks and algae; subtidally it is found on the eelgrass *Zostera* and in the *Macrocystis* canopy offshore. It is not known if the present specimen was associated with drifting algae.

Idotea (Pentidotea) schmitti (Menzies)

Previous distribution: Bering Sea to Monterey Bay, California (Menzies, 1950:171).

New southern record: Punta Banda, Baja del Norte, Mexico; 30 December 1971; D. Conners; one large male from the CAS collection.

Further records: Additional intermediate localities in California include Point Sal (1915, collector unknown) and near Point Conception, Santa Barbara Co. (14–15 July 1916, Carl L. Hubbs). Both lots are from the CAS collection.

Idotea (Pentidotea) stenops (Benedict)

Previous distribution: Coos Bay, Oregon (Hatch, 1947:217) to San Simeon Bay, San Luis Obispo Co., California (Miller, 1968:21).

New southern record: Near Point Conception, Santa Barbara Co., California; 2–3 June and 14–17 July 1916; Carl L. Hubbs; two specimens from the CAS collection.

Synidotea magnifica Menzies and Barnard

Previous distribution: Southern California coastal shelves: Point Conception to Oceanside at depths from 54.9 to 91.5 m (Menzies and Barnard, 1959:26).

New northern record: 6.5 miles, 159° true from Point San Luis Light, San Luis Obispo Bay, California, 35° 3.4' N. Lat., 120° 43.0' W. Long.; 12 September 1938; Crocker-Stanford Expedition; dredged in 36.6 m over fine green mud. One specimen from the CAS collection.

After the acceptance of this paper, I received a copy of the Moss Landing Marine Laboratories benthic survey report (Hodgson, A. T. and J. W. Nybakken, 1973. A Quantitative Survey of the Benthic Infauna of Northern Monterey Bay, California. Moss Landing Marine Laboratories Technical Publication 73-8, 241 pp.). The range extensions for *Haliophasma geminata*, *Gnathia crenulatifrons*, and *Idarcturus allelomorphus* are duplicated here.

ACKNOWLEDGMENTS

I am very grateful to Peter N. Slattery (MLML), James T. Carlton (CAS), David W. Behrens, and John Chapman (California State University, San Francisco) for making their material available. Robert R. Talmadge, of Eureka, California, kindly showed me several rich collecting areas in Humboldt Bay and at Trinidad Head, California. James T. Carlton offered many helpful suggestions on the manuscript.

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ERRATUM

Syvetsen, J. P. 1974. *Relative stem water potentials of three woody perennials in a southern oak woodland community*. Bull. So. California Acad. Sci., 73(2): 108-113. Page 109 (bottom second column) should read as follows:

Relative humidity was recorded daily on a hygrothermograph located 10 km northeast of the site at California Polytechnical University, Pomona (Table 1). Relative humidity was also measured on sampling days at each station with a sling psychrometer. All other climatological data (Tables 2-3) were from the U.S. Dept. of Commerce (1971-72); temperatures were from the Cal Poly Pomona Weather Station and the pre-

cipitation information was from the Walnut Patrol Station Weather Station approximately 4 km north of the site. Both weather stations are located in the same drainage system as the study site but approximately 70 m lower in elevation.

Differences in mean SWP (Figs. 1-6) were statistically analyzed using a randomized complete-block design (Steel and Torrie, 1960) analysis of variance in which the sampling dates were used as blocks.

RESULTS

The data show that the individuals growing at the higher slope positions had significantly

Lines in *italic* moved from page 110 (first column).

RESEARCH NOTES

A NEW SPECIES OF *COMATACARUS* (ACARINA: TROMBICULIDAE) FROM CENTRAL UNITED STATES

Studies of North American chiggers of the subfamily Leeuwenhoeikiinae have revealed a new species of *Comatacarus* Ewing, a genus recently revived by Reed (1973). Examples of this species were reported previously as *Leeuwenhoekia* (*Comatacarus*) *americana* (Ewing) in studies of the larvae (Loomis, 1956, and Finley, 1958) and nymphal stage (Crossley, 1960). The type series is in the University of Kansas chigger collection currently housed at California State University, Long Beach. However, the holotype will be sent, on loan, to the Rocky Mountain Laboratory (RML and USNM). Studies upon which this paper is based were supported by the U.S. Public Health Service Research Grant AI 03407 from the National Institute of Allergy and Infectious Diseases.

Comatacarus pusillus, new species

Figure 1

Types.—Holotype (KU 6171, in RML) plus 4 paratypes (KU 6172–6175) from 24 km N, 19 km W St. Francis, Cheyenne Co, Kansas, from *Peromyscus maniculatus* (RL 521101–14) taken 1.XI.1952 by R. B. Loomis; 4 paratypes (KU 6167–6170) same data as holotype except host *Reithrodontomys megalotis* (RL 521101–15).

Diagnosis.—Palpal setal formula B/B/BBB + 7B; chela with tricuspid cap; galeala branched; 2 genualae I, genuala II and III; tibiala III; subterminala and parasubterminala I; femur I with incomplete suture; sensilla nude; PW/SD = 1.4.

Description of holotype (all measurements in microns with means and extremes of the nine types in parentheses).—Larva; red in life measuring 400 × 270, partially engorged.

Idiosoma: Dorsal body setae arranged 2-44-12-14-14-14-8-6-4 total 118: measurements; humerals 57; anterior dorsal 66–39. Ventral setae 94; measurements; 2 sternal setae 42, 48; preanal setae 27–30, 44; postanal setae 36–42; total body setae 220.

Gnathosoma: palpal setal formula B B BBB + 7B; chela 44, with a tricuspid cap; trifurcate palpal claw; galeala branched.

Scutum: With few and scattered puncta anterior margin biconcave, posterior margin smoothly rounded; AM seta with short accessory branch on basal third; AL bases anterior to AM bases; SB slightly anterior to PL bases; PW/SD = 1.4; sensilla nude.

Scutal measurements: AW 72 (73, 72–75); PW 87 (87, 81–89); SB 30 (27, 21–30); ASB 39 (35, 30–

39); PSB 27 (27, 27–30); AP 39 (38, 36–40); AM 48 (47, 45–50); AL 51 (53, 48–60); PL 45 (48, 45–55); S 84 (84, 78–87); nase 16 × 10.

Legs: 6-6-6 segments, terminating in pair of claws and clawlike empodium, without onychotriches.

Leg I: 360 (350–400); coxa with 2B (branched setae); trochanter with 1B; femur with 1B proximal, incomplete suture; and 5B distal; genu with 4B, 2 genualae, microgenuala; tibia with 8B, 2 tibialae, microtibiala; tarsus 117 × 30 with 40B, tarsala 18 (18–21), microtarsala, parasubterminala, subterminala, pretarsala.

Leg II: 312 (312–355); coxa with 1B; trochanter with 1B; femur with 6B; genu with 4B, genuala, microgenuala; tibia with 6B, 2 tibialae; tarsus 93 × 30 with 25B, tarsala 21 (21–24), microtarsala, pretarsala.

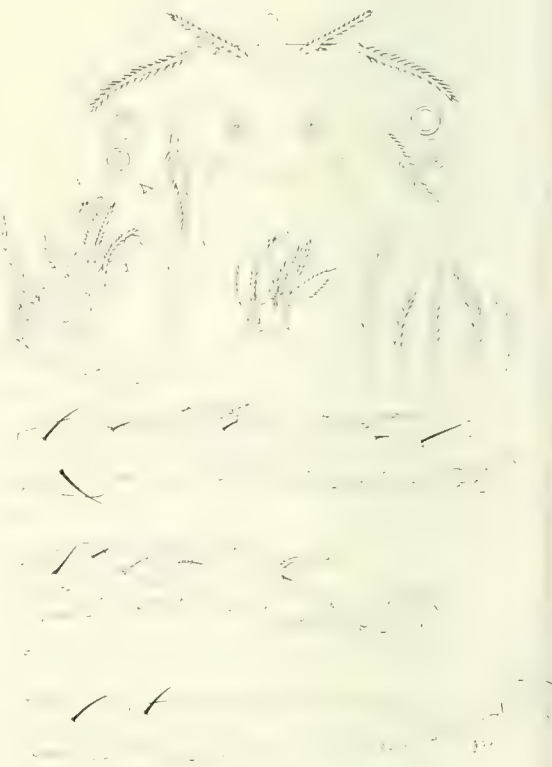


Figure 1. Larva of *Comatacarus pusillus*, new species, A, scutum and eyes; B, dorsal aspect of gnathosoma; C, ventral aspect of palpal tibia and tarsus; D, selected setae (H, humeral; AD, anterior dorsal; PD, posterior dorsal; S, sternal; V, ventral); E, leg I distal three segments showing nude setae with measurements in microns and bases of branched setae; F, leg II as above; G, leg III as above.

Leg III: 378 (354–400); coxa with 1B; trochanter with 1B; femur with 5B; genu with 4B, genuala; tibia with 5B, tibiala; tarsus 114×24 with 18B.

Taxonomic Remarks.—*Comatacarus pusillus* is most closely similar to *C. americanus* Ewing (1942). Examination of the lectotype of *C. americanus* (USNM 1416) revealed that it has a nude lateral palpotibial seta, shorter tarsal segments (I, 60; II, 55; III, 65) and an undivided femur I. Both *C. americanus* and *C. pusillus* have 2 genualae I whereas the other three North American species, *C. stewarti* (Gould), *C. dolosa* (Gould) and *C. inconspicuus* Reed, have only one genuala I. As noted by Vercammen-Grandjean et al. (1973) *C. stewarti* also appears to have a divided femur I.

Reed (1973) restored *Comatacarus* to generic status, and we agree with its removal from *Leeuwenhoekia*, as confirmed by examination of the holotype of the type-species, *L. verduni* (Oudemans).

Reed (1973) reported that all species of *Comatacarus* had an accessory branch on the AM seta. Not only was this character present in *C. pusillus*, it also was seen in three North American species of *Odontacarus*: *O. chiapanensis* (Hoffmann), *O. hirsutus* (Ewing) and *O. villosus* Goff and Loomis, all members of the subgenus *Tarsalacarus* Vercammen-Grandjean.

Crossley (1960) described a nymph, under the name *Leeuwenhoekia americana*, reared from a larva taken with the type series of *C. pusillus*.

Specimens examined (16).—*Comatacarus pusillus* (10): KANSAS. Cheyenne Co, 24 km N, 19 km W St. Francis, 1.XI.1952, *Peromyscus maniculatus* (5, holotype + 4 paratypes), *Reithrodontomys megalotis* (4 paratypes), COLORADO. Boulder Co, 21 km S Estes Park, 8.VIII.1947, *Neotoma cinerea orolestes* (1, KU 6130).

Comatacarus americanus (6): OREGON. Portland, 20.V.1936, western mole (USNM 1416, lectotype + 5).

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BUZZ POLLINATION OF CASSIA QUIEDONDILLA (LEGUMINOSAE) BY BEES OF THE GENERA CENTRIS AND MELIPONA

Van der Pijl (1939), Michener (1962), Linsley (1958, 1962a, b), and Wille (1963) described an effective mode of pollen collection (now termed buzz pollination) that is used by female oligolectic bees while foraging for pollen on flowers having anthers with terminal pores. We now know that hollow, tubular anthers with apical pores are found in at least 400 genera in many plant families (Harris, 1905). Our knowledge of "buzz" (vibratile) pollination is still very incomplete. The present study is a preliminary note on the pollination ecology of an additional *Cassia* species.

Field observations on bee visitations to *Cassia quiedondilla* Micheli, were conducted on 23 January 1974 on the highway midway between Tixtla and Chilapa, in the State of Guerrero, Mexico. Visitations by pollinating bees were observed for two hours, from 1100 to 1300.

Cassia quiedondilla is a large (to 3 m.) caesalpinaceous legume with large yellow flowers (Fig. 1) (Standley, 1927). The flowers are composed of two large curved petals and three highly reduced petals. The larger two petals function in combination as a



Figure 1. *Cassia quiedondilla* (Caesalpinaceae) The flower has four short "fodder" stamens, three short vestigial stamens and three long "pollinating" stamens. *Centris anthracina* Snelling and *Melipona fasciata guerreroensis* Schwarz vibrate their indirect flight muscles to release the pollen from the long curved pollinating anthers.

landing platform and resonating chamber for the bees. There are three large (10 mm.) stamens and four smaller (6 mm.) stamens functioning as "fodder" stamens (Faegri and van der Pijl, 1966; Meeuse, 1961). In addition, there is a third group of three very small (2.5 mm.) rudimentary stamens. The stamens are arcuate and heteranthic. The flowers are a uniform orange-yellow with prominent dark veins, especially in the two large curved petals. There are no markings on the flowers which might function as nectar guides. Pressed voucher specimens of the flowers were photographed under ultraviolet light, using a Sony videorecorder T. V. camera fitted with a U. V. transmitting lens and filter. The flowers proved to be entirely ultra-violet absorptive making the flowers yellow not "bees purple," (Jones and Buchmann, 1974).

The three categories of vibratile pollinators described by Michener (1962), are: 1) the buzzing bees, 2) the biting bees, and 3) the gleaning bees. The two species of bees, *Centris anthracina* Snelling and *Melipona fasciata guerreroensis* Schwarz, which were observed collecting pollen from the flowers of *C. quiedondilla* used only the buzzing technique. Neither biting nor gleaning bees were observed on the flowers, although the time spent watching the pollination interaction was too short.

While working the flowers for the abundant pollen,

both species of bees emitted loud intermittent buzzing sounds which could be heard up to five meters away from the group of *Cassia* plants. The large black *Centris anthracina* is an extremely rapid flier, spending only a few seconds on an individual flower. It produces much louder intermittent buzzes than the smaller *Melipona fasciata guerreroensis*.

The behavior of both *Centris* and *Melipona* is essentially the same on the flowers, although the heavier *Centris* causes the flower to hang in a pendant fashion. The lighter *Melipona* (approximately the size of *Apis mellifera* L.) does not cause this inversion of the flowers. Only female bees were observed in the *Cassia* flowers, since there is no nectar produced to attract male bees. Both bees land on the modified lower petal and move up until the head is positioned at the base of the banner petal. Curling their bodies tightly over the long pollinating anthers, the bees vibrate their indirect flight muscles (wings are held closed over the back) in one to three extremely short bursts of high (higher than normal flight sounds) frequency sounds. This vibration of the flower results in loosening of the pollen and it shoots out of the terminal anther pores in the form of a small cloud. Most of the small light pollen is lost in this manner, but much of the pollen lands on the ventral part of the bee's thorax and abdomen. After receiving pollen on its venter, the bee backs out of the flower and in mid-air combs the pollen into the scopa.

Previous studies have indicated that some *Solanum* species produce an unusually high percentage of inviable (judged by staining with cotton-blue) pollen grains (Linsley and Cazier, 1963). Linsley and Cazier reported testing pollen loads from *Solanum elaeagnifolium* pollinators and found that 64 percent of the pollen grains were inviable. They suggested that the high proportion of inviable pollen grains was due to some inherent genetic factor and not the result of high external temperatures as reported by Stow (1927). When mixed populations of *S. rostratum* and *S. elaeagnifolium* were tested, Linsley and Cazier (1963, 1970) reported that the percentage of inviable grains was only 15.6 percent of the total. In *Solanum douglassii* Dunal, Jones, and Buchmann (unpublished) found that only 5 percent of the pollen produced was inviable.

Cassia quiedondilla produces an extremely high percentage of inviable pollen grains. Tests made using a cotton-blue with lactophenol stain, revealed that inviable pollen averaged 92.6 percent of that pollen produced by the three anther types. The normal pollinating anthers produced 95 percent inviable pollen (549 grains counted), while the "fodder" anthers tested revealed that 96 percent were inviable (500 grains counted) and the rudimentary anthers produced 87 percent inviable pollen (500 grains counted). As reported by various writers, *Cassia* produces two sizes of pollen grains. Linsley and Cazier (1972), have reported that *Cassia bauhinioides*

produced 79 percent of the small-grained type (2,565 grains counted). The large grains were about 80 microns in diameter, whereas the small grains were only 27 microns in diameter. The large grains in *C. quiedondilla* are 32.5 microns in diameter and the smaller grains are 20 microns in diameter. These abundant small but viable pollen grains have been interpreted by Linsley and Cazier (1972) as a food "bonus" for pollinating bees. The ratio of small pollen grains in *C. quiedondilla* was found to be 43.4 percent of the 1,949 grains counted. Undoubtedly, these pollen grains act as an extra food reward for pollinating bees.

In addition, the presence of 43.4 percent small grains in the *Cassia* anthers may function as billiard balls and serve to loosen more of the pollen from the anthers. When the anthers are vibrated, the smaller grains would serve to knock more of the pollen out into the pollen cloud that is characteristic of buzz pollination in species of *Solanum* and *Cassia*.

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As indicated in the Instructions for Authors (inside back cover), all manuscripts submitted to SCAS BULLETIN are reviewed by referees who critically read for scientific content, originality, and clarity of presentation, and who assist the editor in making judgments as to acceptability for publication. The reviewers also assist authors by offering constructive suggestions which may lead to improvement of the text or illustrations of manuscripts. By contribution of their time and professional expertise the referees measurably enhance the quality of SCAS BULLETIN.

In behalf of our readers, authors, and myself, I thank the following reviewers for valuable editorial assistance in recent months: Phillip A. Adams, James

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Technical sessions—Anthropology, Archaeology, Botany, Earth Science, Entomology, Experimental Biology, Folklore, History, Invertebrate Zoology, Marine Science, Vertebrate Zoology,

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Banquet—The annual banquet will be held the evening of May 10; presentation of awards will be made at this time.

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COVER: Three female and three male California grunion, *Leuresthes tenuis*, spawning in the sand at Doheny Beach, California. Females are buried tail first in the sand, males are lying horizontally near them.

Photo by Michael H. Horn, Dept. of Biological Sciences, California State University, Fullerton.

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